ACCOUNT NO

TITLE NO

STYLE

SLOT

SPINE LETTERING

ISSN

NAME

University of Illinois/Ur
Library Binding Division
1408 W. Gregory Drive
Urbana, IL 61801

PERIODICAL		BOOK
VOL. / YR	FREQUENCY	

☐ PERM. CHANGE
☐ NEW TITLE

		RECASE
TITLE PAGE		MOUNT COVER
TABLE CONT.		POCKET / CLOTH
INDEX		POCKET / PAPER
FRONT COVER		
BACK COVER		
ADS		

☐ STANDARD BOOK   ☐ FLEX-S
☐ CUSTOM BOOK   ☐ FLEX-M
☐ THESIS   ☐ MUSIC
☐ DUSTIE   ☐

INSTRUCTIONS TO BINDERY:
1BIX   2NIX   3NIX
NARROW MARGINS

FIELDIANA

ECOLOGY

NO. 88-95

1993-95

89-95

v. 88-95

3

4

5

6

7

8

9

241 11/01
18838
124 8U1
ICI
INFORMATION
CONSERVATION, INC

BINDERY COPY Item:

Lot: 991   Shipment:
71

COVER COLOR	SET OF
990	
PRINT COLOR	
W	F

BINDERY USE ONLY

HAND TRIM	☐	STF	☐
RECASE	☐	STUB	☐
EXTRA TIME			MIN.
REASON			
OTHER			

FIELDIANA

Zoology
NEW SERIES, NO. 90

A Floral and Faunal Inventory of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar: With Reference to Elevational Variation

Steven M. Goodman, Editor

Information for Contributors to Fieldiana

A Floral and Faunal Inventory of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar

WWF

FIELDIANA

Zoology
NEW SERIES, NO. 90

A Floral and Faunal Inventory of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar: With Reference to Elevational Variation

Steven M. Goodman, Editor

Center for Environmental and Evolutionary Biology
Field Museum of Natural History
Roosevelt Road at Lake Shore Drive
Chicago, Illinois 60605
U.S.A.

World Wide Fund for Nature
B. P. 738
Antananarivo (101)
Madagascar

PUBLISHED BY FIELD MUSEUM OF NATURAL HISTORY

Contents

Preface

This volume contains reports of the results of a biological inventory of the Réserve Spéciale (RS) d'Anjanaharibe-Sud, in northeastern Madagascar, conducted by 11 biologists in October and November 1994. This inventory was the second large-scale elevational transect organized under the auspices of the World Wide Fund for Nature (WWF), Madagascar, with the first being in the Réserve Naturelle Intégrale (RNI) d'Andringitra in the southeast. Since the RS d'Anjanaharibe-Sud survey, we have conducted a similar inventory in the RNI d'Andohahela, in the extreme southeast, and we are now making final arrangements for a survey of the slopes of the RNI de Marojejy, northeast of the RS d'Anjanaharibe-Sud. Each of these sites is the focal point of a conservation project associated with a protected area and organized by WWF in collaboration with the Malagasy government.

The principal aims of these elevational transects are to provide the local conservation project with basic information on the fauna and flora of each protected area, to study the distribution of numerous plants and animals along an elevational gradient, and to examine possible ecological correlates in the altitudinal zonation of these organisms. As we survey more mountains, we will be able to compare patterns of the elevational distribution of organisms between sites and along a latitudinal gradient from approximately 14°S to 23°S latitude.

The RS d'Anjanaharibe-Sud survey was conducted between the end of the austral winter and the start of the rainy season. The survey team moved in unison up the slopes of the reserve. The only exception was a follow-up herpetological study of the western slopes of the reserve conducted in late January to mid-February 1996. The period from October to December is the best possible for a multidisciplinary biological inventory in the humid forests of eastern Madagascar because the greatest reproductive activity of many organisms occurs at this time and because many organisms are more conspicuous (e.g., singing birds) or more easily identified (e.g., plants in flower or fruit) during their reproductive season.

We attempted to gather data using standardized techniques. In the future our exercise can be repeated to determine whether there have been any clear differences in the biotic diversity of the sites visited that might be correlated with stochastic or human-induced environmental change. Having stated that, it is important to emphasize that our inventory of the RS d'Anjanaharibe-Sud was conducted during a relatively short period of time, and, as is the case with any rapid assessment, the results should not be construed as definitive. Rather, our survey provides baseline information on which future studies can build.

S. M. Goodman

May 1998
Chicago, Illinois

Chapter 1

Description of the 1994 Biological Inventory of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar

Steven M. Goodman[1]

The Réserve Spéciale (RS) d'Anjanaharibe-Sud is located in northeastern Madagascar and centered at 14°42'S latitude and 49°26'E longitude (Fig. 1-1). This reserve of humid forest comprises an area of approximately 32,100 ha over the elevational range of 500–2064 m. The reserve was created in 1958. The western part is in the Province of Mahajanga and the eastern part is in the Province of Antsiranana (Nicoll & Langrand, 1989).

A multinational and multidisciplinary group of biologists studied the fauna and flora of the reserve from 15 October to 30 November 1994. Four camps were placed at different elevations (875, 1260, 1550, and 1950 m), and transects were centered around these sites at an altitudinal limit of ±75 m elevation. We gathered data to examine the relationship of the fauna and flora along an elevational gradient, particularly with regard to altitudinal distributions and species turnover. This study was parallel to transects conducted in the RNI d'Andringitra in late 1993 (Goodman, 1996) and in the RNI d'Andohahela in late 1995 (Goodman, in prep.).

Abbreviations Used in the Text

ANGAP	Association Nationale pour la Gestion des Aires Protégées
CNRS	Centre National de la Recherche Scientifique
dbh	diameter at breast height
DEF	Direction des Eaux et Forêts
FTM	Foiben-Taosarintanin'i Madagasikara (Institut National de Géodesie et Cartographie)

FMNH	Field Museum of Natural History
MBG	Missouri Botanical Garden
MNHN	Muséum National d'Histoire Naturelle, Paris
PBZT	Parc Botanique et Zoologique de Tsimbazaza
PN	Parc National
RB	Réserve de Biosphère
RCP	La Recherche Coopérative sur Programme No. 225, under the Centre National de la Recherche Scientifique
RNI	Réserve Naturelle Intégrale
RS	Réserve Spéciale
UMMZ	University of Michigan Museum of Zoology
WWF	World Wide Fund for Nature

Transect Sites

Coordinates were determined with the use of a geographical position system, the geographical names from various maps (Institut Géographique National, 1964; FTM, 1977), and consultation with local people. Altitude was determined with altimeters. The positions of each camp and the major trail systems are presented in Figure 1-1.

875 m (camp 1)—Madagascar: Province d'Antsiranana, Réserve Spéciale d'Anjanaharibe-Sud, 6.5 km SSW of Befingotra, 14°45.3'S, 49°30.3'E.

1260 m (camp 2)—Madagascar: Province d'Antsiranana, Réserve Spéciale d'Anjanaharibe-Sud, 9.2 km WSW of Befingotra, 14°44.7'S, 49°27.7'E.

1550 m (camp 3)—Madagascar: Province d'Antsiranana, Réserve Spéciale d'Anjanaharibe-

[1] Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, IL 60605-2496, U.S.A.
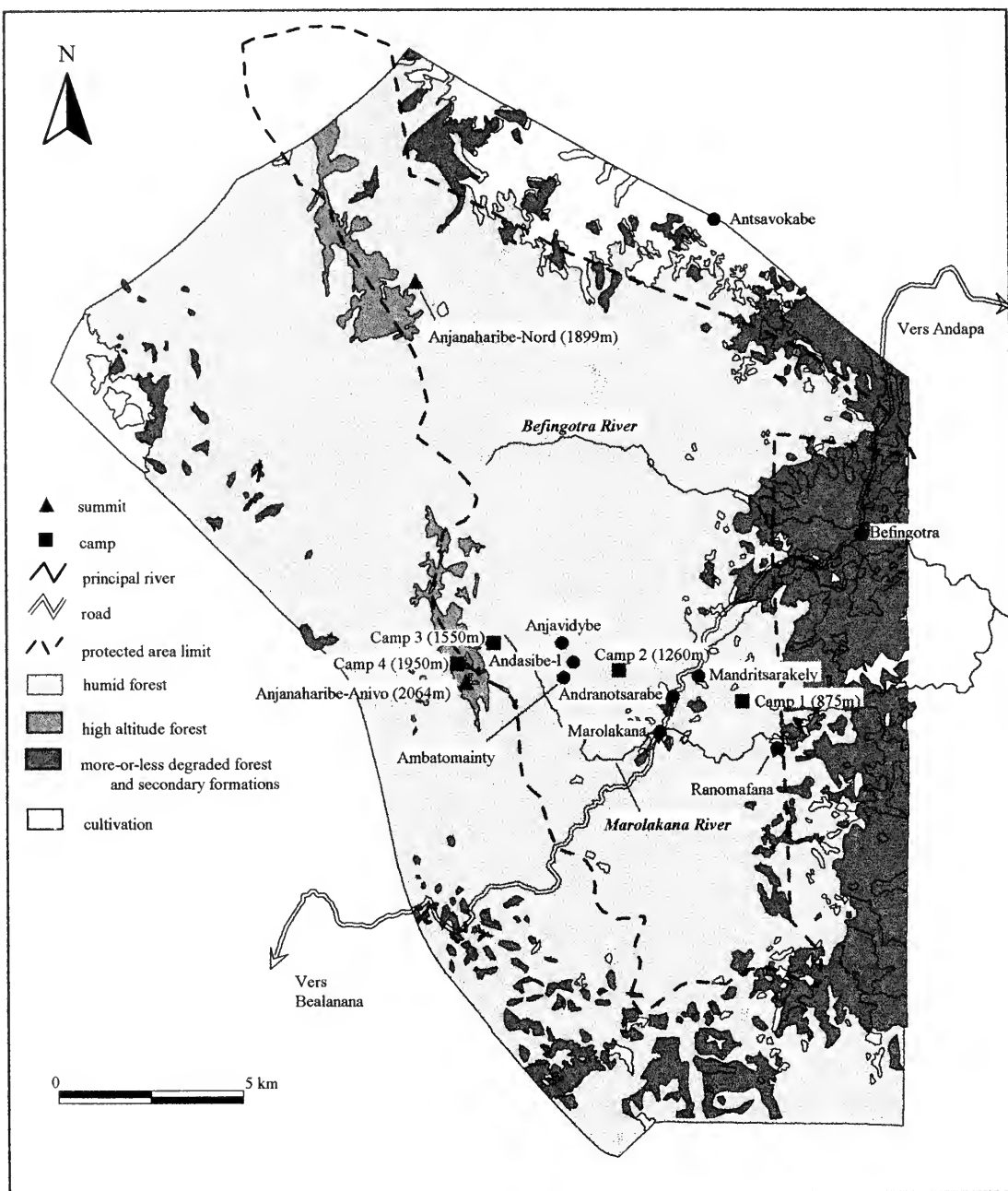
FIG. 1-1. Map of the RS d'Anjanaharibe-Sud and surrounding areas. Positions of the camp sites used during the 1994 elevational transect of the region are indicated.

Sud, 11 km WSW of Befingotra, 14°44.5'S, 49°26.5'E.

1950 m (camp 4)—Madagascar: Province d'Antsiranana, Réserve Spéciale d'Anjanaharibe-Sud, 12.2 km WSW of Befingotra, 14°44.8'S, 49°26.0'E.

Itinerary of the 1994 Expedition

RECONNAISSANCE—Reconnaissance (13–19 September 1994) was conducted by Goodman and Ravokatra to determine the route to be used for the elevational transect.

FIG. 1-2. Site within the RS d'Anjanaharibe-Sud and between Anjavidy Be and the Marolakana River exploited for quartz. The bank was cut away to expose a vein of crystal. This technique results in considerable erosion and in vegetation, including large trees, sliding down slopes. (Photograph by B. Fisher.)

FIELD TRIP—During the field trip (15 October–30 November 1994), scientific members included Fisher (ants), Goodman (small mammals, bats, and birds), Hawkins (birds), Rabibisoa (reptiles and amphibians), Raharimalala (ferns), Rakotondrainibe (ferns), Ravokatra (birds), Schmid (lemurs), Smolker (lemurs), and Thiollay (birds for the 875 m and 1260 m transects). The dates for each transect were as follows: 16–31 October, 875 m transect; 1–14 November, 1260 m transect; 14–23 November, 1550 m transect; and 23–30 November, 1950 m transect.

A list of all field and laboratory participants in this project is presented in Appendix 1-1.

Logistics and Trail Systems

During the past few years a new road has been built that runs westward from Andapa to Bealanana and passes directly through the RS d'Anjanaharibe-Sud. Thus, this reserve, which was once somewhat isolated, is now accessible by motor vehicle. The road passes from Befingotra into the Marolakana Valley, up over the flank of the massif, and down the western slopes. Our first camp was located in the forested area south of the new road and about 1.5 km above the small village of Ranomafana (along the Marolakana River). The site was accessible via a small trail that connects the villages of Mandritsarakely and Ranomafana. This zone of forest contained numerous paths, and no new trails were cut.

The second elevational transect zone was along the trail that connects the village of Andranotsarabe (along the main road) to the ridge peak within the RS d'Anjanaharibe-Sud called Anjavidy Be. The camp was located along the Ambatomainty River about 2 km below and southeast of an area of at least 5 ha, called Ambatomainty, that has been heavily mined in recent years for different types of quartz crystal. The principal techniques of exploitation are to dig narrow tunnels, often meters deep

FIG. 1-3. Marolakana River along the trail between Anjavidy Be and camp 3 (1550 m). (Photograph by B. Fisher.)

and just big enough for a person to crawl in, in the soil following veins of rock, and to cut away large banks of soil to expose quartz deposits (Fig. 1-2). These techniques result in considerable erosion damage, exposed tree roots, and many tree falls. This elevational zone had relatively extensive trail systems, and no new paths were cut.

Access to the third elevational transect zone was along an established trail from Ambato-mainty up a slope to the top of the ridge at An-javidy Be (1540 m), west and down to the Mar-olakana River valley, across the valley (Fig. 1-3), and back up to a saddle on a ridge leading toward the summit of Anjanaharibe Anivo. The trail be-

Fig. 1-4. Slope above camp 3 (1550 m) leading toward the summit of Anjanaharibe Anivo. The actual summit is hidden behind the outcrop (upper left). As one moves up the slope, the forest structure shifts from being mostly closed canopy to open canopy with widely spaced trees and finally to ericoid shrubs adjacent to and above the open outcrop. (Photograph by B. Fisher.)

tween Ambatomainty and Anjavidy Be was rel-
atively open, and only a few stretches needed to
be cleared. The trail from Anjavidy Be to the
Marolakana River had been used for quartz ex-
ploitation several years ago, but extensive
lengths of it needed to be reopened. A complete-
ly new trail was cut from the Marolakana River
to our 1550 m transect zone (camp 3). All of the
transect trails used in this elevation zone were
cut by expedition members.

The fourth camp (1950 m) was located just
below the ecotone between closed canopy forest
and ericoid savannah in a shallow protected sad-
dle a few hundred meters from a steep ridge de-
scending into the Marolakana Valley (Fig. 1-4).
From this vantage point to the east one could see
across the Andapa Basin to the jagged peaks of
the RNI de Marojejy (Fig. 1-5). The trail be-
tween camp 3 and camp 4 as well as the trails
to the summit zone and for transects were cut by
the survey team.

Meteorology

The variation in the biological communities of
the RS d'Anjanaharibe-Sud is related to the mas-
sif's orographic position and elevational gradient.
The eastern edge of the reserve is about 75 km
from the seacoast. Tropical weather systems
sweeping westward across the Indian Ocean pass
over the eastern coast of Madagascar and then in-
land (Donque, 1975). The high mountains of the
island act as a partial barrier to the passage of
these systems further westward. The Anjanahari-
be-Sud Massif is a primary example of such a
barrier, with the eastern side receiving more pre-
cipitation than the western side.

During the 1994 mission to the reserve, data
were collected on the minimum and maximum
daily temperatures (°C) and daily precipitation
(mm). These data were collected each morning
between 07:00 and 08:30 hr. The minimum and
maximum temperatures and precipitation data

Fig. 1-5. View toward the east from near camp 4 (1950 m) across the slopes above the Marolakana River and Andapa Basin (below clouds) toward the jagged peaks of the RNI de Marojejy. (Photograph by A. F. A. Hawkins.)

TABLE 1-1. Summary of minimum and maximum temperatures and precipitation during 1994 expedition to RS d'Anjanaharibe-Sud.

Period of measure- ment at each camp	Temperature (°C)*		Rainfall (mm)†
	Minimum	Maximum	
875 m			
16–31 Oct.	15, 15–17	15, 20–24	8, 0.5–17.5
	15.5, 1.1	21.0, 0.9	8.3, 6.8
1260 m			
1–14 Nov.	13, 12–15	13, 17–23	11, 1.0–15.0
	13.1, 1.2	19.6, 1.7	6.8, 4.5
1550 m			
14–23 Nov.	9, 8–12	8, 24–31	0
	11.3, 1.8	21.6, 4.9	
1950 m			
23–30 Nov.	7, 8.5–13	6, 17–21	3, 3.0–15.0
	11.8, 1.4	18.5, 1.4	8.2, 5.0

* Data are presented as number of records, range, mean, and SD.

† Data are presented as number of days with rain, range, mean, and SD.

gathered between 16 October and 30 November 1994 are presented in Table 1-1 and are divided into the periods during which each of the transect zones was visited. In general, the average daily minimum and maximum temperatures decreased with altitude. Precipitation was highly variable and not clearly correlated with elevation. No exceptionally heavy rainfall occurred during the expedition; the greatest cumulative amount during a 24-hr period was 17.5 mm.

Literature Cited

DONQUE, G. 1975. Contribution géographique à l'étude du climat de Madagascar. Nouvelle Imprimerie des Arts Graphiques, Antananarivo, vii + 478 pp.

FTM. 1977. Andapa, 1:100,000, feuille W-36. Foiben Taosarintanin'i Madagasikara, Antananarivo.

GOODMAN, S. M., ED. 1996. A floral and faunal inventory of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madgascar: With reference to elevational variation. Fieldiana: Zoology, n.s. **85:** 1–319.

INSTITUT GÉOGRAPHIQUE NATIONAL. 1964. Ambodisa-

trana, 1:100,000, feuille V-38. Institut Géographique National, Paris.

Nicoll, M. E., and O. Langrand. 1989. Madagascar: Revue de la conservation et des aires protégées. World Wide Fund for Nature, Gland, xvii + 374 pp.

Appendix 1-1
Participants in the Project
(Field and Laboratory)

A total of 18 field workers and scientists took part in this multidisciplinary study. This total included the field participants listed in the previous section as well as researchers responsible for some of the laboratory studies. The names and addresses of all scientific participants follow:

Andreone, F., Museo Regionale di Scienze Naturali, Via G. Giolitti, 36, 10123 Torino, Italy.

Carleton, M. D., Division of Mammals, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A.

Fisher, B. L., Department of Entomology, University of California, Davis, California 95616, U.S.A. *Current address:* Life Sciences Division, South African Museum, P.O. Box 61, 8000 Cape Town, South Africa.

Goodman, S. M., Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, Illinois 60605, U.S.A., and World Wide Fund for Nature, Aires Protégées, B.P. 738, Antananarivo (101), Madagascar.

Hawkins, A. F. A., B.P. 8511, Antananarivo (101), Madagascar. *Current address:* World Wide Fund for Nature, B.P. 738, Antananarivo (101), Madagascar.

Jenkins, P. D., Mammal Group, The Natural History Museum, Cromwell Road, London SW7 5BD, United Kingdom.

Lewis, B. A., Missouri Botanical Garden, B.P. 3391, Antananarivo (101), Madagascar.

Lourenço, W. R., Laboratoire de Zoologie (Arthropodes), Muséum National d'Histoire Naturelle, 61, rue de Buffon, 75005 Paris, France.

Nussbaum, R. A., Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48109-1079, U.S.A.

O'Connor, B. M., Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48109-1079, U.S.A.

Rabibisoa, N., Département de Biologie Animale, B.P. 906, Université d'Antananarivo, Antananarivo (101), Madagascar.

Raharimalala, F., Service de Biologie et Physiologie Végétale, Université d'Antananarivo, B.P. 906, Antananarivo (101), Madagascar.

Randriamahazo, H., Parc Botanique et Zoologique de Tsimbazaza, B.P. 4096, Antananarivo (101), Madagascar.

Rakotondrainibe, F., Laboratoire de Phytomorphologie, Ecole Pratique des Hautes Etudes, 16, rue de Buffon, 75005 Paris, France.

Ravokatra, M., World Wide Fund for Nature, B.P. 738, Antananarivo (101), Madagascar.

Raxworthy, C. J., Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48109-1079, U.S.A. *Current address:* Center for Environmental Research and Conservation, Columbia University, 1200 Amsterdam Avenue, New York, New York 10027, U.S.A.

Schmid, J., Deutsches Primatenzentrum, Kellnerweg 4, Göttingen 37077, Germany, and Abteilung für Verhaltensphysiologie, Beim Kupferhammer 8, 72070 Tübingen, Germany.

Smolker, R., Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48109-1079, U.S.A.

Thiollay, J.-M., Laboratoire d'Ecologie, Ecole Normale Superieure, 46, rue d'Ulm, 75230 Paris, Cedex 05, France.

Chapter 2

Description of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar

Steven M. Goodman[1] and Beverley A. Lewis[2]

Setting and Geology

The Réserve Spéciale (RS) d'Anjanaharibe-Sud lies along a chain of mountains composed of quartzitic and granitic rock (Petit, 1971) with steep slopes and numerous flanks and covered with humid forests (Humbert, 1955a) that descend into the lowlands. The reserve is to the west of the Andapa Basin. The Lokoho River, which starts along the eastern slopes of the reserve as the Marolakana River and subsequently the Ankaibe River (Chaperon et al., 1993), provides freshwater for numerous villages and towns within the region and for irrigation of crops. To the northeast of the basin lie the mountains of the Réserve Naturelle Intégrale (RNI) de Marojejy. The highest peak within the RS d'Anjanaharibe-Sud is Anjanaharibe Anivo, at 2064 m, and there are at least two other peaks above 2000 m (Institut Géographique National, 1964). In the RNI de Marojejy, the highest peak is 2132 m (FTM, 1977).

No meteorological station exists in the immediate vicinity of the RS d'Anjanaharibe-Sud. The closest station is in the Andapa Basin, from which the following information was obtained (Randriamaherisoa et al., 1993). The region is characterized by a humid and tropical climate. The mean temperature ranges from 18°C in July to 25°C in February (the warmest month). The relative humidity is generally about 87% but reaches 97% in March and April. The annual precipitation is slightly more than 2 m, 65% of which falls during the rainy season between December and March. On average it rains 271 days per year. During the rainy season, the region experiences devastating cyclones.

The Andapa Basin, one of the major rice-producing centers of Madagascar, has experienced considerable silting over the past two decades, largely as a result of erosion on surrounding hillsides caused by deforestation (Neuvy, 1979; Randriamaherisoa et al., 1993). Since 1957 there have been significant decreases in the regional forest cover and extent of marshland. Between 1957 and 1978 there was an increase in rice production under paddy and slash-and-burn (*tavy*) cultivation, and by 1990 rice cultivation had decreased, largely due to siltation (Table 2-1). Between 1957 and 1990 there was a steady expansion of coffee and vanilla plantations (Table 2-1). On the national scale, the reduction of rice production in the Andapa Basin is a serious matter, and one of the goals of the integrated conservation and development project of the World Wide Fund for Nature (WWF) in the region is to ameliorate this problem (Berner, 1995).

TABLE 2-1. Changes in land cover in the Andapa Basin (total surface area, 1050 km²) between 1957 and 1990 (based on Randriamaherisoa et al., 1993).

	Coverage (%)*		
Land cover	1957	1978	1990
Forest	77.8	48.7	55.1
Tavy/savoka	6.9	31.2	20.1
Coffee and vanilla	5.3	7.1	13.8
Habitation	0.4	0.9	1.3
Paddy rice	2.8	10.7	8.0
Marshland	5.8	—	1.7

* Percentage of basin area.

[1] Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, IL 60605-2496 U.S.A.
[2] Missouri Botanical Garden, B.P. 3391, Antananarivo (101), Madagascar.

FIG. 2-1. Forest within the 875 m elevational zone. Note relatively high density of understory trees. (Photograph by B. Fisher.)

Previous Research Conducted in the Reserve and the Immediate Region

Little scientific research has been conducted within the RS d'Anjanaharibe-Sud. As part of a review of the protected areas system of Madagas-

car, Nicoll and Langrand (1989) briefly visited the site to obtain general information on the fauna, flora, condition, and human pressures. They also published a list of the known vertebrates, largely birds and lemurs, of the reserve based on their own observations and interviews with local peo-

FIG. 2-2. View looking west from Anjavidy Be across the Marolakana River valley to the hills south of the 1550 m camp. Areas on the far hills devoid of trees are the result of rockfalls. Such sites often have thick growths of bamboo. (Photograph by A. F. A. Hawkins.)

ple. The only previously published study we are aware of for vertebrates within the reserve was of *Indri indri* (Thalmann et al., 1993).

In contrast to the RS d'Anjanaharibe-Sud, the RNI de Marojejy, just across the Andapa Basin, has been the site of relatively numerous scientific activities. The initial exploration of this region was conducted by the botanist H. Humbert (1955b). Subsequently there were several visits to the area by entomologists (Griveaud, 1960). In the late 1960s, as part of La Recherche Coopérative sur Programme (RCP) No. 225, under the auspices of the Centre National de la Recherche Scientifique, France, a multidisciplinary group of scientists visited the RNI de Marojejy to study aspects of the geomorphology, climate, fauna, and flora (Guillaumet et al., 1975). The collections made during the RCP mission provided material for numerous subsequent taxonomic studies, for example, studies of the reptiles of the region (Brygoo et al., 1970a,b).

In more recent years the RNI de Marojejy has been the site of several zoological and botanical

expeditions. Starting in 1987 various portions of the massif have been explored, and plants have been collected by botanists from and associated with the Missouri Botanical Garden (MBG). A checklist of the known flora of the reserve is currently under preparation by Jim Miller and colleagues. University student expeditions from the United Kingdom visited the reserve in 1988 (Safford & Duckworth, 1990) and in 1989 (Pont & Armstrong, 1990), primarily to study birds and bats, respectively. Furthermore, the former expedition resulted in several other papers about the birds (Sheldon & Duckworth, 1990) and lemurs (Duckworth, 1993; Duckworth et al., 1995) of the reserve.

Floristics

During the 1994 survey of the RS d'Anjanaharibe-Sud, there was no detailed botanical survey such as was conducted in the RNI

FIG. 2-3.   Forest near the 1550 m camp. Note the heavier moss and epiphyte loads on the vegetation in comparison to the 875 m zone (Fig. 2-1). (Photograph by B. Fisher.)

d'Andringitra (Lewis et al., 1996). In several of the transect zones in the RS d'Anjanaharibe-Sud, parataxonomists associated with a collaborative project between WWF and MBG made general plant collections. Information on aspects of the reserve's floristic structure and utilization of forest products by local villagers is contained in Raza-kanaivo (1995). Furthermore, at the end of the survey, Lewis visited our four camp sites to provide qualitative descriptions of the flora along the elevational transect. The following descriptions are based largely on her visit to the reserve.

Fig. 2-4. Upper limit of the forested zone on Anjanaharibe-Sud at approximately 1980 m. In the background is the closed-canopy forest, which grades into mixed pockets of closed-canopy forest and open ericoid brush toward the foreground. (Photograph by B. Fisher.)

The vegetation of the 875 m transect zone can be characterized as follows. The canopy height was between 25 and 30 m. The large tree flora was rich and diverse and was composed of the following families: Burseraceae (*Canarium*), Elaeocarpaceae (*Sloanea*, which were usually buttressed trees), Lauraceae, Clusiaceae, Annonaceae, Sapindaceae, Moraceae (*Ficus*), and Bignoniaceae (*Phyllarthron*). Smaller trees, 15–20 m high, included Rubiaceae, Ebenaceae, Oleaceae, Araliaceae, Euphorbiaceae (*Uapaca*), Sterculiaceae (especially *Dombeya*), Monimiaceae (*Tambourissa*), Rutaceae, Pittosporaceae, Anacardiaceae, Myrtaceae, and Sapindaceae (*Tina*). A large number of these trees were cauliflorous, which is often linked to high rainfall (G. Schatz, pers. comm.). Lianas were common, and the following were present: Rubiaceae (*Danais*), Apocynaceae (*Landolphia*), Fabaceae (*Strongylodon*), and Sterculiaceae (*Byttneria*). Epiphytes included a relatively rich fern flora (see Chapter 3), orchids, Piperaceae (*Piper*), and Araceae (*Pothos scandens* L.). In the shrub layer, Myrsinaceae

(*Oncostemum*) was abundant, as was Rubiaceae (*Psychotria*). Herbs included orchids, Lamiaceae, Balsaminaceae (*Impatiens*), and Melastomataceae (*Grevesia*). The parasitic family Balanophoraceae (*Balanophora*) was also growing in the camp area. Within this transect zone there were areas of previously exploited forest that were in an advanced stage of regeneration and dominated by *Harungana* (Guttiferae). Portions of the forest were dominated by dense areas of relatively small trees (Fig. 2-1).

The vegetation in the 1260 m zone had a structure similar to that in the 875 m zone, with large trees attaining a height of 25–30 m and the same general generic composition. *Sloanea* and *Canarium* were abundant, along with members of the families Clusiaceae and Sapindaceae. The smaller trees, 15–20 m in height, included *Uapaca*, which was common and easily recognized by its stilted roots. Other abundant families included Clusiaceae, Apocynaceae, Araliaceae, Monimiaceae, Myrtaceae, Ebenaceae, Flacourtiaceae, Oleaceae, Anacardiaceae, and Moraceae (*Ficus*). Lianas

FIG. 2-5.   Dense moss and epiphyte cover in the closed-canopy forest at 1950 m. (Photograph by B. Fisher.)

were common. Epiphytes were abundant, with ferns and orchids predominating. The parasitic Loranthaceae (*Bakerella*) was also seen.

The vegetation within the 1550 m transect zone was remarkable for still having some large trees, such as *Sloanea*, up to 18 m high on relatively flat, sheltered ground. *Canarium* dropped out at

about 1300 m. The average height of the trees at 1550 m was about 10–15 m and distinctly shorter than that within the lower transects. Common families of canopy trees were Rubiaceae, Euphorbiaceae (*Croton, Alchornea*), Araliaceae (*Polysias*), Asteraceae (*Vernonia, Apodocephela*), Flacourtiaceae (*Apholia*), Myrtaceae, Verbenaceae,

FIG. 2-6. Open ericoid bush just below the summit of Anjanaharibe-Sud at about 2000 m. The landscape in this area is spotted with a few 3- to 5-m-tall trees. (Photograph by S. M. Goodman.)

Canellaceae (*Cinnamosma*), Rutaceae (*Zanthoxylum*), and Clusiaceae (*Symphonia*). Small trees and shrubs, generally 2–4 m high, included Rubiaceae, Cyathaceae, and Myrsinaceae (*Oncostemum*). Bamboo was common, especially in open areas of natural rockfall or gaps (Fig. 2-2). An endemic shrub or small tree, *Ascarina coursii* (Humb. & Cap.) Leroy & Jérémie (Chloranthaceae), a plant that grows in the high-altitude forests of Marojejy and Anjanaharibe-Sud massifs, was found in this zone. It has an unusual range as the center of distribution of this genus is in Melanesia, Polynesia, and New Zealand (Jérémie, 1980). Epiphytic moss and lichen were abundant on the tree trunks and branches (Fig. 2-3). Other common epiphytes were orchids and Melastomataceae (*Medinilla*). Herbs included Araceae (*Arophyton rhizomatosum* (S. Buchet) Bogner), Balsaminaceae (*Impatiens*), Gesneriaceae (*Streptocarpus*), and Bignoniaceae.

The tallest trees near the 1950 m camp, just at the ecotone between the upper forest limit and ericoid scrub, were approximately 4 m high. Here, the canopy structure was different from that at lower elevations, having only one stratum and trees with more branches closer to the ground. The majority of the leaves were sclerophyllous. Trunks and branches of trees and virtually all other types of surfaces were covered in epiphytic moss and lichen due to the frequent mist and cloud cover (Figs. 2-4, 2-5). Asteraceae, Clusiaceae (*Symphonia*), Rubiaceae, and Cunoniaceae (*Weinmannia*) were common, as were *Medinilla* and *Bakerella*. In some areas bamboo was abundant, and in more open areas *Philippia* (Ericaceae) was the dominant shrub. The tree line occurred just above the camp at about 1980 m. Above this point to the summit (2031 m), the vegetation was ericaceous bush, up to 1.5 m high, with abundant *Philippia*, herbaceous Asteraceae (*Senecio, Helichrysum*), Balsaminaceae (*Impatiens*), Ericaceae (*Vaccinium secundiflorum* Hook.), and shrubs of Araliaceae, Clusiaceae, and Cunoniaceae (*Weinmannia*) (Fig. 2-6). There was no large area of bare rock in the summit zone.

Literature Cited

BERNER, P. O. 1995. Préparation d'un volet forestier au sein d'un projet de conservation et développement in-

tégré de la région est de Madagascar: Le cas du complexe des réserves de Marojejy et d'Anjanaharibe-Sud. Akon'ny Ala, **17:** 28–39.

BRYGOO, E. R., C. P. BLANC, AND C. A. DOMERGUE. 1970a. Notes sur les *Brookesia* de Madagascar: III. *Brookesia karchei* n. sp. du Massif du Marojezy. Annales d'Université de Madagascar (Sciences), **7:** 267–271.

———. 1970b. Notes sur les *Chamaeleo* de Madagascar: IV. *C. gastrotaenia* n. subsp. du Massif du Marojezy. Annales d'Université de Madagascar (Sciences), **7:** 273–278.

CHAPERON, P., J. DANLOUX, AND L. FERRY. 1993. Fleuves et Rivières de Madagascar. Monographies Hydrologiques no. 10. ORSTOM, Paris, 874 pp.

DUCKWORTH, J. W. 1993. Feeding damage left in bamboos, probably by aye-ayes (*Daubentonia madagascariensis*). International Journal of Primatology, **14:** 927–931.

DUCKWORTH, J. W., M. I. EVANS, A. F. A. HAWKINS, R. J. SAFFORD, AND R. J. WILKINSON. 1995. The lemurs of Marojejy Strict Nature Reserve, Madagascar: A status overview with notes on ecology and threats. International Journal of Primatology, **16:** 545–559.

FTM. 1977. Andapa, 1:100,000, feuille W-36. Foiben-Taosarintanin'i Madagasikara, Antananarivo.

GRIVEAUD, P. 1960. Une mission zoologique de l'IRSM au Marojejy. Naturaliste Malgache, **12:** 43–55.

GUILLAUMET, J.-L., J.-M. BETSCH, C. BLANC, P. MORAT, AND A. PEYRIÉRAS (sous la direction de R. PAULIAN). 1975. Étude des écosystèmes montagnards dans la région malgache. III. Le Marojezy. IV. L'Itremo et l'Ibity. Géomorphologie, climatologie, faune et flore (Campagne RCP 225, 1972–1973). Bulletin du Muséum National d'Histoire Naturelle, série 3, **309** (Écologie générale 25): 29–67.

HUMBERT, H. 1955a. Les territoires phytogéographiques de Madagascar. *In* Les divisions écologiques du monde. Colloques Internationale, Centre National de Recherche Scientifique, **59:** 195–204.

HUMBERT, H. 1955b. Une merveille de la nature à Madagascar: Première exploration de massif du Marojejy et des ses satellites. Mémoires Institut Scientifique de Madagascar, série B, **6:** 1–210.

INSTITUT GÉOGRAPHIQUE NATIONAL. 1964. Ambodisatrana, 1:100,000, feuille V-38. Institut Géographique National, Paris.

JÉRÉMIE, J. 1980. Notes sur le genre *Ascarinia* (Chloranthaceae) en Nouvelle-Calédonie et à Madagascar. Adansonia, série 2, **20**(3): 273–285.

LEWIS, B. A., P. B. PHILLIPSON, M. ANDRIANARISATA, G. RAHAJASOA, P. J. RAKOTOMALAZA, M. RANDRIAMBOLOLONA, AND J. F. MCDONAGH. 1996. A study of the botanical structure, composition, and diversity of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar, pp. 24–72. *In* Goodman, S. M., ed., A floral and faunal inventory of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: With reference to elevational variation. Fieldiana: Zoology, n.s., **85:** 1–319.

NEUVY, G. 1979. Amenagement régional à Madagascar—La cuvette d'Andapa. Madagascar Revue de Géographie, **35:** 55–139.

NICOLL, M. E., AND O. LANGRAND. 1989. Madagascar: Revue de la conservation et des aires protégées. World Wide Fund for Nature, Gland, xvii + 374 pp.

PETIT, M. 1971. Contribution à l'étude morphologique des reliefs granitiques à Madagascar. Imprimerie Centrale, Tananarive, 308 pp.

PONT, S. M., AND J. D. ARMSTRONG. 1990. A study of the bat fauna of the Réserve Naturelle Intégral [sic] de Marojejy in north-east Madagascar: Report of the Aberdeen University Expedition to Madagascar 1989. Department of Zoology, University of Aberdeen, Aberdeen, 57 pp.

RANDRIAMAHERISOA, A., M. BINARD, AND E. PERSOONS. 1993. Use of G.I.S. and remote sensing in hydrological model for impact study of land cover change in a Malagasy rural basin. EARSeL Advances in Remote Sensing, **2**(3): 154–164.

RAZAKANAIVO, V. L. 1995. Contribution à l'analyse de l'occupation du sol dans la Réserve Spéciale d'Anjanaharibe-Sud et sa zone peripherique en vue d'une gestion rationnelle des ressources naturelles. Mémoire de fin d'études. Ecole Supérieure des Sciences Agronomiques, Département des Eaux et Forêt, Université d'Antananarivo, Antananarivo, 105 pp.

SAFFORD, R., AND W. DUCKWORTH, EDS. 1990. A wildlife survey of Marojejy Nature Reserve, Madagascar: Report of the Cambridge Madagascar Rainforest Expedition, 1988. Study Report no. 40. International Council for Bird Preservation, Cambridge, 172 pp.

SHELDON, B. C., AND J. W. DUCKWORTH. 1990. Rediscovery of the Madagascar Serpent-eagle *Eutriorchis astur*. Bulletin of the British Ornithologists' Club, **110:** 126–130.

THALMANN, U., T. GEISSMANN, A. SIMONA, AND T. MUTSCHLER. 1993. The Indris of Anjanaharibe-Sud, northeastern Madagascar. International Journal of Primatology, **14:** 357–381.

Chapter 3

The Pteridophytes of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar: Floristic Analysis and Altitudinal Distribution

France Rakotondrainibe[1] and Fidèle Raharimalala[2]

Abstract

The pteridophyte flora of the Réserve Spéciale d'Anjanaharibe-Sud is exceptionally rich: 211 species or varieties belonging to 60 genera were collected along the southeastern slopes between 600 and 2000 m. Of these pteridophytes, 82 are endemic to Madagascar, five species (four of which have not been described) are presently considered endemic to the massif, and *Xiphopteris sikkimensis* (an Asian species) is reported for the first time from Madagascar.

The generic and specific floristique composition varied with altitude. The genera *Asplenium* and *Trichomanes* show the highest diversity between 800 and 1250 m; the genera *Elaphoglossum*, *Huperzia*, *Grammitis*, *Ctenopteris*, and *Hymenophyllum* exhibit the greatest diversity between 1250 and 1650 m. The overall highest species richness is between 1250 and 1350 m. Terrestrial and lithophytic pteridophytes are more abundant at lower elevations. After 820 m epiphytic ferns and fern allies dominate the pteridophyte flora.

The floristic data obtained from 12 plots of 300 to 800 m² were analyzed using two types of multivariate techniques (AFC and CAH) that differentiated three different groups along the southeast slopes of the reserve: lower elevations (600–1200 m), middle elevations (1250–1650 m), and upper elevations (1900–2000 m). The characteristic taxa of each group are enumerated. At low elevations a topographic gradient running from valley floors to ridges is superimposed, on the altitudinal floristic gradient.

Résumé

La flore ptéridologique de la Réserve Spéciale d'Anjanaharibe-Sud est exceptionellement riche et originale: 211 espèces ou variétés réparties en 60 genres ont été recensées sur le versant Sud-Est, entre 600 et 2000 m d'altitude. Parmi elles: 82 sont endémiques de Madagascar, cinq espéces (dont quatre à décrire) sont considérées à ce jour comme endémiques du massif, et *Xiphopteris sikkimensis* (espèce asiatique) est signalée pour la première fois à Madagascar.

La composition floristique générique et spécifique varie avec l'altitude. Les genres *Asplenium* et *Trichomanes* sont les plus diversifiés entre 800 et 1250 m; les genres *Elaphoglossum*, *Huperzia*, *Grammitis*, *Ctenopteris*, et *Hymenophyllum* sont les plus diversitiés entre 1250 et 1650 m. La richesse spécifique est maximale entre 1250 et 1350 m. Les ptéridophytes terrestres et éphilithes sont les plus abondantes à basse altitude; à partir de 820 m les ptéridophytes éphiphytes sont toujours dominantes.

---

[1] Laboratoire de Phytomorphologie, Ecole Pratique des Hautes Etudes, 16, rue Buffon, 75005 Paris, France.
[2] Service de Biologie et Physiologie Végétale, Université d'Antananarivo, B.P. 906, Antananarivo (101), Madagascar.

Les données floristiques relevées sur 12 parcelles de 300 à 800 m² et traitées par deux types d'analyses multivariables complémentaires (AFC et CAH) permettent de distinguer trois groupements différents le long du versant Sud-Est de la réserve: le groupement de l'étage altitudinal inférieur (600–1020 m), celui de l'étage de moyenne altitude (1250–1650 m), et celui de l'étage altitudinal supérieur (1900–2000 m). Les taxa caractéristiques de chaque groupement sont énumérés. A ce gradient floristique altitudinal se superpose, à basse altitude seulement, un gradient floristique topographique, de la vallée jusqu'à la crête.

Introduction

Little information has been published to date on the pteridophytes of the Anjanaharibe chain. During 1950–1951 Humbert devoted 3 weeks to botanical exploration in the upper valley of the Andramonta River and the northern Anjanaharibe Massif during his eighth trip to Madagascar, accompanied by Capuron and Cours. This work was conducted in an area to the northwest of the limit of the Réserve Spéciale (RS) d'Anjanaharibe-Sud, at the latitude of the village of Ambohisatrana. The 43 species of ferns collected during this expedition are deposited at the Muséum National d'Histoire Naturelle in Paris and were cited in the *Flore de Madagascar et des Comores* (Tardieu-Blot, 1951–1971). Information is provided on the altitude at which each specimen was collected, but there is no indication of the frequency or the habit of the species. This first inventory, which was far from exhaustive, nevertheless shows the botanical interest of the region. Among the 43 pteridophytes species collected by Humbert, two of them, *Lindsaea humbertii* (Tardieu) Kramer and *Diplazium andapense*,[3] are considered endemic to the Anjanaharibe Chain; *Ctenopteris torulosa*, a species known from Réunion Island, has been recorded in Madagascar only from the Anjanaharibe Massif; and three species, *Lindsaea coursii* (Tardieu) Kramer, *Lonchitis coriacea* Tardieu, and *Blechnum madagascariense*, are endemic to the region, having been collected only in the Anjanaharibe chain and the nearby Marojejy Massif.

Apparently, no other works have been published on the flora of the RS d'Anjanaharibe-Sud. To our knowledge, only one botanical expedition, focused primarily on flowering plants, was conducted in the reserve before our study, during that expedition, which was conducted by B. Lewis (MO) and personnel from the World Wide Fund for Nature (WWF) in March 1994, only one pteridophyte belonging to the genus *Huperzia* was

collected (TROPICOS database, MO). Inventory work currently being carried out in the area by a WWF staff member, with assistance from MO, should add to our botanical knowledge of the reserve.

Field work for the present study was conducted in October and November 1994 as part of a multidisciplinary biological inventory of the eastern and southeastern slopes of the RS d'Anjanaharibe-Sud. Our role was to study the diversity and altitudinal distribution of the pteridophyte species occurring in the area.

Methods

The overall inventory of the pteridophyte species, presented in Table 3-1, includes information from all of the collections and observations made only during this expedition, from the banks of the Marolakana River, located at 600 m altitude, to the summit zone, at 2000 m (see Chapter 1). It also includes floristic data taken from the sample plots established for the quantitative studies described below. Complete sets of voucher specimens have been deposited at the herbarium of the Département des Recherches Forestières et Piscicoles, Centre National de la Recherche Appliquée au Développement, (FOFIFA). Antananarivo, (TEF) and at the Laboratoire de Phanérogamie, Museum National d'Histoire Naturelle, Paris (P); duplicate specimens will also be sent to Missouri Botanical Garden, St. Louis (MO) and to the Royal Botanic Gardens, Kew.

In the majority of cases the genera treatments recognized follow those used in African literature (Schelpe, 1970; Burrows, 1990; Johns, 1991). However, genera divisions in Thelypteridaceae and in Grammitidaceae follow those proposed by Holttum (1974) and Pichi-Sermolli (1977), respectively. The division of Lycopodiaceae into four genera, detailed by Øllgaard (1989), is adopted. Only one genus, *Cyathea*, is recognized in the

No. code	Taxa*	Altitudinal distribution†					Biology‡
		600–700 m	820–1020 m	1250–1350 m	1550–1650 m	1900–2000 m	
1	*Amauropelta bergiana* (Schltdl.) Holttum			●	+++		T
2	**Antrophyum bivittatum** C.Chr.			●			E
3	*Antrophyum boryanum* (Willd.) Kaulf.		++	+++	++		E, r
4	*Antrophyum immersum* (Willd.) Mett.	●	●				E, r
5	**Antrophyum malgassicum** C.Chr.	●	+	●			E, r
6	*Arthropteris monocarpa* (H.L. Cordem.) C.Chr.	●	+++	+++	+++		E, r
7	*Arthropteris orientalis* (J.F.Gmel) Posth.	●	++				E, r
8	**Arthropteris parallela** C.Chr.			+	●		E
9	*Asplenium aethiopicum* (Burm.f.) Bech.			●	+		E
10	*Asplenium* aff. *anisophyllum* Kunze (FR 2112, 2138, 2228, 2250)	+	++				E, r
11	**Asplenium affine** Sw. var. **gilpinae** (Baker) Tardieu		●				T
12	**Asplenium afzelii** Rosend.		●				E
13	*Asplenium auritum* Sw.			●			E
14	*Asplenium bipartitum* Bory ex Willd.	++++	+++				E, r
15	*Asplenium cancellatum* Alston		+	+++		+	T, E, r
16	*Asplenium cuneatum* Lam.	+++	+++				E, r
17	*Asplenium friesiorum* C.Chr.			++	+		E
18	**Asplenium herpetopteris** Baker var. **acutipinnatum** (Bonap.) Tardieu			●			T
19	**Asplenium herpetopteris** Baker var. **herpetopteris**		+++	+++	+++	●	E, r
20	**Asplenium herpetopteris** Baker var. **massoulae** (Bonap.) Tardieu		●	+++	++	+	T, E, r
21	**Asplenium herpetopteris** Baker var. **villosum** (Bonap.) Tardieu		+++				E, r
22	*Asplenium inaequilaterale* Willd.	+	++				R
23	**Asplenium lokohoense** Tardieu			+			E
24	**Asplenium marojejyense** Tardieu	+++					R
25	*Asplenium monanthes* L.			++	+		T, r
26	*Asplenium nidus* L.	+++	+++	●			E, r
27	*Asplenium normale* D.Don			+	++	+++	T, E, r
28	*Asplenium obscurum* Blume		++	++			T, r
29	*Asplenium pellucidum* Lam.	++	+++				E, r
30	*Asplenium petiolulatum* Mett.		++	+	●		E
31	**Asplenium poolii** Baker		●	++	++		E
32	*Asplenium sandersonii* Hook.		+	+++	+++		E
33	*Asplenium unilaterale* Lam.	+++	++	++			T, r
34	*Asplenium variabile* Hook. var. *paucijugum* (F.Ballard) Alston	++					T
35	*Athyrium scandicinum* (Willd.) C.Presl			+++	+++	+++	T
36	*Belvisia spicata* (L.f.) Mirb.		++	●			E
37	*Blechnum attenuatum* (Sw.) Mett.		+	+++	+++	++++	T, E
38	**Blechnum humbertii** Tardieu					+	T
39	*Blechnum ivohibense* C.Chr.			+++			T
40	**Blechnum madagascariense** Tardieu		+		++	+++	T, E
41	**Blechnum simillimum** (Baker) Diels	++	+++	+++			T, E, r
42	**Blechnum simillimum** (Baker) Diels f. **binerve** (Hook.) Tardieu		++	+++	+++		T, E, r
43	**Blechnum simillimum** (Baker) Diels f. **xiphophyllum** (Baker) Tardieu		●				T
44	**Blechnum sp. nov.** 1 (FR 2548)			●			T
45	**Blechnum sp. nov.** 2 (FR 2384)			●			T
46	**Blotiella madagascariensis** (Hook.) Tryon		+	+++	+++	+++	T
47	*Bolbitis auriculata* (Lam.) Alston	++					T
48	*Christella dentata* (Forssk.) Brownsey & Jermy	●	+				T

TABLE 3-1. *Continued.*

No. code	Taxa*	Altitudinal distribution†					Biology‡
		600–700 m	820–1020 m	1250–1350 m	1550–1650 m	1900–2000 m	
49	*Christella distans* (Hook.) Holttum	+	+++	+++	+++		T
50	*Cochlidium serrulatum* (Sw.) L.E.Bishop		●	●			E
51	**Coniogramme madagascariensis** C.Chr.			++	+++		T
52	*Ctenitis* aff. *crinita* (Poir.) Ching (FR 2172)	●	●				T
53	*Ctenitis cirrhosa* (Schumach.) Ching	+					T
54	**Ctenitis madagascariensis** Tardieu			●			T
55	**Ctenitis ochrorachis** (Baker) Tardieu		+	+++			T
56	**Ctenopteris alboglandulosa** (Bonap.) Tardieu				●		E
57	**Ctenopteris deltodon** (Baker) Tardieu				+++	+	E
58	*Ctenopteris devoluta* (Baker) Tardieu		●	+++	+++	++	E
59	*Ctenopteris elastica* (Bory) Copel.	●	++	+++	●		E, r
60	*Ctenopteris flabelliformis* (Poir.) J.Sm.				●	+++	E
61	**Ctenopteris humbertii** (C.Chr.) Tardieu					++	E
62	*Ctenopteris torulosa* (Baker) Tardieu (FR 2458)				●		E
63	*Ctenopteris villosissima* (Hook.) Harley		●	+++	+++	+++	E
64	**Ctenopteris zenkeri** (Hieron.) Tardieu	●	+	++	●		E
65	*Cyathea* aff. *hildebrandtii* Kuhn (FR 2096)	●	+++	+	●	+++	T
66	*Cyathea* aff. *similis* C.Chr. (FR 2339)			+	●		T
67	**Cyathea auriculata** Tardieu		●	+++	+++		T
68	**Cyathea bellisquamata** Bonap. var. **basilobata** C.Chr.				++	+	T
69	**Cyathea borbonica** Desv. var. **laevigata** Bonap.	●	+				T
70	*Cyathea bullata* (Baker) Rakotondr.			+++	+++	+++	T
71	**Cyathea costularis** Bonap.				+++		T
72	**Cyathea coursii (Tardieu) Rakotondr.**				+++		T
73	**Cyathea decrescens** Mett.		++	+++			T
74	**Cyathea dregei** Kunze var. **polyphlebia** C.Chr.			+++	●	●	T
75	*Cyathea hildebrandtii* Kuhn		●	+	●	+	T
76	**Cyathea longipinnata** Bonap.		+				T
77	**Cyathea melleri** (Baker) Domin var. **melleri**		●	●			T
78c	**Cyathea melleri** (Baker) Domin var. **virescens** (C.Chr.) Tardieu		+				T
79	**Cyathea serratifolia** Baker	+	+++				T
80	**Cyathea sp. nov.** (FR 2524)					●	T
81	**Cyathea tsaratanensis** Tardieu		●		●		T
82	*Davallia chaerophylloides* (Poir.) Steu.	●	+++		●		E
83	*Deparia* sp. (FR 2177, 2253)	●	+	+	●		T
84	*Dicranopteris linearis* (Burm.f.) Underw.				●		T
85	**Didymochlaena microphylla** (Bonap.) C.Chr.			++			T
86	**Diplazium andapense** (Tardieu) Rakotondr.			●	+++		T
87	*Diplazium proliferum* (Lam.) Thouars	+	+				T
88	**Diplazium zakamenense** (Tardieu) Rakotondr.	+	+++		+++	+	T
89	*Drynaria willdenowii* (Bory) T. Moore		+++				E
90	**Dryopteris mangindranensis** Tardieu			++	++	+++	T
91	**Dryopteris remotipinnula** Bonap.					+++	T
92	*Elaphoglossum acrostichoides* (Hook. & Grev.) Schelpe				++	+++	E
93	*Elaphoglossum* aff. *angustatum* (FR 2272, 2289 bis)			+++	+++	+++	E
94	*Elaphoglossum* aff. *macropodium* (Fée) T. Moore (FR 2158, 2224)		●				E
95	*Elaphoglossum* aff. *zakamenense* Tardieu (FR 2121)		●				E
96	*Elaphoglossum angulatum* (Blume) T. Moore				●	+++	T
97	*Elaphoglossum aubertii* (Desv.) T. Moore			●	++	+++	E, r
98	**Elaphoglossum coriaceum** Bonap.		+++	+			E
99	**Elaphoglossum decaryanum** Tardieu			●			E

TABLE 3-1. *Continued.*

No. code	Taxa*	Altitudinal distribution†					Biology‡
		600–700 m	820–1020 m	1250–1350 m	1550–1650 m	1900–2000 m	
100	*Elaphoglossum deckenii* (Kuhn) C.Chr. var. *rufidulum* (Willd. ex Kuhn) Tardieu	●	+	+++	+++	+++	E, r
101	**Elaphoglossum humbertii** C.Chr.		●	+	+++	++	E
102	*Elaphoglossum hybridum* (Bory) Brack.		●				E
103	*Elaphoglossum lepervanchii* (Fée) Moore		●	●			E
104	**Elaphoglossum leucolepis** (Baker) Krajina ex Tardieu		●	+++	●		E
105	*Elaphoglossum marojejyense* Tardieu			+			E
106	*Elaphoglossum petiolatum* (Sw.) Urb. ssp. *salicifolium* (Willd. ex Kaulf.) Schelpe			+	+	●	E, r
107	**Elaphoglossum scolopendriforme** Tardieu		+++	+++	+++		E
108	*Elaphoglossum sieberi* (Hook. & Grev.) T. Moore		+++	+++	+		E
109	**Elaphoglossum sp. nov.** (FR 2270, 2469, 2480)			+++	+++	+++	E
110	*Elaphoglossum spathulatum* (Bory) T. Moore	●					R
111	**Elaphoglossum subsessile** (Baker) C.Chr.		+++	++	++	+	T, E
112	*Elaphoglossum* aff. *welwitschii* (Baker) C.Chr.				+++		E
113	*Gleichenia polypodioides* (L.) J.E.Smith					+	T, R
114	*Grammitis barbatula* (Baker) Copel.			●	●	+	E
115	**Grammitis copelandii** Tardieu				++	+++	E
116	*Grammitis cryptophlebia* (Baker) Copel.			●	+++	+++	E
117	**Grammitis gilpinae** (Baker) Tardieu			+	+++		E
118	**Grammitis holophlebia** (Baker) Copel.			+++	+++	++++	E
119	*Grammitis kyimbilensis* (Brause) Copel.				+++	++	E
120	*Grammitis obtusa* Willd. ex Kaulf.				+++		E
121	**Grammitis sp. nov.** (FR 2500, 2526)					●	E
122	*Grammitis synsora* (Baker) Copel.		●	●			E
123	*Histiopteris incisa* (Thunb.) J.Sm.			+++			T
124	*Humata repens* (L.f.) Diels		●				E
125	**Huperzia gagnepainiana** (Herter) Tardieu				●		E
126	*Huperzia gnidioides* (L.f.) Trevis					+	E
127	**Huperzia megastachya** (Baker) Tardieu	●	+	●			E, R
128	*Huperzia obtusifolia* (P. Beauv.) Rothm.				+		E
129	*Huperzia ophioglossoides* (Lam.) Rothm.			●			E
130	**Huperzia pecten** (Baker) Tardieu		●	+			E
131	*Huperzia squarrosa* (G.Forst.) Trevis.			++	●	+++	E
132	**Huperzia trigona** (C.Chr.) Tardieu			+	+++	++	E
133	*Huperzia verticillata* (L.f.) Trevis.				●		E
134	**Hymenophyllum** aff. **ivohibense** Tardieu (FR 2511, 2541)					++++	E
135	*Hymenophyllum capense* Schrad.		●	●	+++	++++	E
136	*Hymenophyllum capillare* Desv. var. (FR 2348, 2446)			●	+++		E
137	**Hymenophyllum heimii** Tardieu			+	●		E
138	*Hymenophyllum hirsutum* (L.) Sw.		++	+++	+++	+++	E, r
139	**Hymenophyllum humbertii** C.Chr.			●		+++	E
140	*Hymenophyllum inaequale* (Poir.) Desv.			●		●	E
141	**Hymenophyllum perrieri** Tardieu			+++	●		E
142	*Hymenophyllum polyanthos* (Sw.) Sw.		●	+++	+++	++++	E
143	**Hymenophyllum polyanthos** (Sw.) Sw. var. **kuhnii** (C.Chr.) Schelpe				●		E
144	**Hymenophyllum poolii** Baker			+	+	+++	E, r
145	*Hymenophyllum sibthorpioides* Mett.		++	+++	+++	+++	E
146	*Hymenophyllum tunbrigense* (L.) Smith			●	●	+++	E
147	**Hymenophyllum veronicoides** C.Chr.			●			E
148	*Hypolepis sparsisora* (Schrad.) Kuhn			++			T
149	**Lastreopsis boivinii** (Baker) Tardieu				+++		T

TABLE 3-1.   *Continued.*

No. code	Taxa*	Altitudinal distribution†					Biology‡
		600–700 m	820–1020 m	1250–1350 m	1550–1650 m	1900–2000 m	
150	*Lastreopsis subsimilis* (Hook.) Tindale			•			T
151	***Lindsaea blotiana*** K.U.Kramer		+++	+++			T, r
152	***Lindsaea flabellifolia*** (Baker) Kuhn		•	•			T
153	***Lindsaea goudotiana*** (Kunze) Kuhn			+++			E
154	*Lindsaea madagascariensis* Baker		•	+++	+++		T
155	***Lomariopsis crassifolia*** Holttum		•	+			T, E, R
156	*Loxogramme lanceolata* (Sw.) C.Presl.	+	++	+	+		R, E
157	*Lygodium lanceolatum* Desv.	+	+++				L
158	*Marattia fraxinea* Sm. ex J.F.Gmel.	+	+				T
159	*Megalastrum lanuginosun* (Kaulf.) Holttum		+				T
160	***Microlepia madagascariensis*** C.Presl.	+	+++				T
161	*Microsorun punctatum* (L.) Copel.	+++	++				E, r
162	*Monogramma graminea* (Poir.) Schkuhr		•				E
163	*Nephrolepis biserrata* (Sw.) Schott	++++	+++				T, r
164	*Nephrolepis tuberosa* (Bory) C.Presl			•			E
165	*Oleandra distenta* Kunze	•	+++	+++	+++	•	E, r
166	*Phymatosorus scolopendria* (Burm.f.) Pic. Serm.	+++	+++				E, r
167	*Pityrogramma argentea* (Willd.) Domin					•	T, r
168	***Platycerium madagascariense*** Baker		++				E
169	*Pleopeltis excavata* (Bory ex Willd.) Sledge		++	•	+++	+	E
170	*Pleopeltis macrocarpa* (Bory ex Willd.) Kaulf.		•				E
171	*Pleopeltis schraderi* (Mett.) Tardieu				•		E
172	***Pneumatopteris remotipinna*** (Bonap.) Holttum	+	++				T
173	*Pneumatopteris subpenningera* (C.Chr.) Holttum		+++	+	•		T
174	*Pseudocyclosorus pulcher* (Willd.) Holttum				++		T
175	*Pseudophegopteris cruciata* (Willd.) Holttum			+++	+		T
176	*Pteris catoptera* Kunze		+++				T
177	***Pteris elongatiloba*** Bonap. var. ***remotivenia*** Bonap.	+++	+++				T
178	***Pteris heteroclita*** Desv.	•					T
179	*Pteris pseudolonchitis* Bory ex Willd.			+++	•	•	T
180	*Pteris remotifolia* Baker			+++	+++	+	T
181	*Pteris woodwardioides* Bory ex Willd.	+++	+++				T
182	*Pyrrosia rhodesiana* (C.Chr.) Schelpe		•				E
183	*Rumohra adiantiformis* (G.Forst.) Ching	++	+++		+++	++++	T, E, r
184	***Rumohra lokohoensis*** Tardieu			+++			E
185	***Saccoloma henriettae*** (Baker) C.Chr.	•	•	+++	+++		T
186	*Schizaea dichotoma* L.		+++	•			T
187	*Selaginella fissidentoides* (Hook. & Grev.) Spring		++++				T
188	***Selaginella pectinata*** Spring		++++	++			T
189	*Selaginella unilateralis* Spring			+++			T, r
190	*Sphaerostephanos arbuscula* (Willd.) Holttum	•					T
191	*Sticherus flagellaris* (Bory) St.John				•		T
192	*Trichomanes* aff. *cupressoides* Desv. (FR 2362, 2467)		+	+	+		T, r
193	*Trichomanes* aff. *rigidum* Sw. (FR 2533, 2097)		+++	+++	•	•	T, r
194	*Trichomanes bipunctatum* Poir.	+++	+++	•			E, r
195	*Trichomanes bonapartei* C.Chr.		++	+	+		E, r
196	*Trichomanes borbonicum* Bosch	•	+++	+++	+++	++++	E, r
197	*Trichomanes cupsidatum* Willd.	•	+	++	+		E, r
198	*Trichomanes digitatum* Sw.		+	+++	+		E
199	*Trichomanes erosum* Willd.		•				E
200	*Trichomanes lenormandii* Bosch		+++	+++	+++		E, r
201	***Trichomanes longilabiatum*** Bonap.	•					R
202	*Trichomanes meifolium* Bory ex Willd.			++			T, r
203	*Trichomanes montanum* Hooker		•	+++			E
204	*Trichomanes speciosum* Willd.		•	+++			L

TABLE 3-1. *Continued.*

No. code	Taxa*	Altitudinal distribution†					Biology‡
		600–700 m	820–1020 m	1250–1350 m	1550–1650 m	1900–2000 m	
205	*Vittaria elongata* Sw.		●				E
206	*Vittaria ensiformis* Sw.	+	+	●			E, r
207	*Vittaria humblotii* Hieron.		●	+++	+++		E
208	*Vittaria isoetifolia* Bory ex Fée			●			E
209	*Vittaria scolopendrina* (Bory) Thwaites	●					R
210	**Xiphopteris oosora** (Baker) Alston var. **micropecten** C.Chr.				++	+++	E
211	*Xiphopteris sikkimensis* (Hieron.) Copel.				●	++++	E

* Endemic species are indicated by bold type.

† ● = very rare (observed only once); + = rare (observed two to five times); ++ = infrequent (observed six to 20 times); +++ = frequent (observed 21 to 50 times); and ++++ = very frequent (observed >50 times).

‡ T = terrestrial species; E = epiphytic species; R = strictly epilithic species; r = occasionally epilithic species; and L = lianescent species.

Cyatheaceae according to Holttum (1981) and Kramer in Kubitzki (1990).

The quantitative study, involving the establishment of sample plots, was designed to enable the characterization of pteridophyte floristic composition at different altitudinal zones. The plots were centered around each camp within the following elevational ranges: 820–1020 m (camp 1), 1250–1350 m (camp 2), 1550–1650 m (camp 3), and 1900–2000 m (camp 4). To obtain results that could be compared with data from similar work conducted in other protected areas within Madagascar, the methodology used at Anjanaharibe-Sud followed that of previous studies (Rakotondrainibe, 1989; Rahajasoa, 1993; Rakotondrainibe & Raharimalala, in press). Field work within each elevational zone involved two stages.

1. During preliminary study (2–3 days), plants were observed and collected in an area of 1–2 km around the camp, using primarily the transect trails established for other members of the expedition. This work made it possible to evaluate the diversity of the local biotopes and to compile a list of the species occurring within the altitudinal zone. For each species observed (Table 3-1), a value was assigned (1–5) to indicate the frequency with which it occurred (see Table 3-1 for definitions).

2. During the following 3–6 days, the number of species (species richness) and the total number of individuals of each species (abundance) were counted in sample plots measuring between 300 and 800 m². The methodology used for these plot studies is described below.

Number of Plots and Choice of Placement

Forest structure and composition within a given altitudinal zone are not homogeneous. In general they constitute a mosaic of elements whose distribution is discontinuous and repetitive in space and that in an area with broken relief, such as the RS d'Anjanaharibe-Sud, is usually determined as a function of topography (Duvigneaud, 1955, 1980; Rakotondrainibe & Guillerm, 1990). To assess diversity in these ecological conditions, it is necessary to place a sample plot in as many elements of the mosaic as possible, for example, on a ridge line, a middle slope, a lower slope, a valley bottom, and along a watercourse.

In the RS d'Anjanaharibe-Sud, this approach was followed between 860 and 1350 m. At higher altitudes, above 1500 m, the methodology was modified because watercourses are temporary, irregular, and generally dry or reduced to a small flow, and because the forests occurring on the lower and middle slopes are homogeneous in structure and composition. For these reasons, above 1650 m, only two plots were established, one on a ridge and the other on a slope (Table 3-2, plots 9 and 10).

Because field time was limited, it was not possible to conduct quantitative analyses of specialized biotopes, whose distribution is related to local conditions rather than topography, such as forest gaps in which heliophilous species occur or large rock outcrops found near summit areas, which have specialized flora. The plants present in these habitats were, however, included in the

TABLE 3-2. Characteristics of RS d'Anjanaharibe-Sud study plots on slopes.

Characteristic	Plot									
	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10
Area, m²	800	800	800	800	700	700	800	700	300	800
Altitude, m	900	830	1000	1320	1260	1230	1570	1600	2000	1930
Topographic position	Middle slope	Lower slope	Ridge	Ridge	Middle slope	Lower slope	Middle slope	Ridge	Ridge	Middle slope
Exposure	SSE	SE	SE	S	E	E	ESE	ESE	SSE	ESE
Slope	Average	Average	Gentle	Very gentle	Very gentle	Steep	Steep	Very gentle	Very gentle	Average
Canopy height, m	25	15–20	20	20	15	20	15	10	3	8
Woody plant cover, %	60–80	60–65	60–70	40–50	40–45	60–65	40–45	40	30–40	25–35
Herbaceous plant cover, %	15–20	15–25	15–20	20–35	30–40	35	30–35	35	80–90 (moss)	70–80 (moss)
Litter thickness, cm	3–10	6–10	8–14	10–20	5–10	5–15	5–10	2–30	0 (moss)	5–15
Humus thickness, cm	0	1	0–1	20–30	7–15	10	10–25	20–40	Variable (0–?)	5–20
Soil	Yellow-ocre clay	Brown clay	Light brown clay	Yellow-ocre clay	Yellow-ocre clay-sand	Yellow-ocre clay	Yellow-ocre clay	Very rocky	Yellow-ocre clay	Whitish gray clay-sand

Plot	Area (m²)	Altitude (m)	Width of stream bed (m)	Nature of stream bed	Slope	Flow
R1	800 (200 × 4)	850	1–3	Large granitic rocks + sand	Gentle	Very gentle
R2	800 (200 × 4)	1250	3–5	Large granitic rocks + gravel + sand	Gentle	Very gentle

overall inventory (Table 3-1), and their frequency was estimated.

Plot Area

The first criteria taken into consideration in de-limiting each plot were the homogeneity of the vegetation and the physical characteristics of the area. As has often been indicated by various authors (Guinochet, 1973; Vanden Berghen, 1973; Godron et al., 1983), the notion of homogeneity is somewhat subjective, although in practice, with sufficient field experience, it can be applied with satisfactory results. In the present study, we focused on the physiognomy and structure of the vegetation; the floristic composition of the terrestrial and epiphytic pteridophytes and of the dominant flowering plants in the canopy and understory layers; and the physical features of the site, such as the slope, exposure, soil structure, and moisture.

Within an area considered to be homogeneous on the basis of these criteria, the size and placement of each study plot were selected to include all (or nearly all) of the species present within the particular element of the vegetational mosaic to be sampled. The studies cited above have shown from other humid forests in Madagascar that the minimal area needed for a representative sample of pteridophytes, as indicated by species–area curves, is between 500 and 1000 m², depending on the diversity of the biotope (Rakotondrainibe, 1989). Considering that in mountainous areas the difficulty in delimiting large plots of homogeneous vegetation increases with higher elevation, we chose a standard plot size of 800 m² whenever the topography of the sample area allowed. Three of the 12 plots established (P5, P6, and P8), however, are only 700 m² each, and plot P9, located at 2000 m altitude on a narrow ridge in a floristically impoverished formation, covered only 300

m². However, species abundance figures, determined using values from 1 to 6 on a nonlinear scale (see below), were always calculated on the basis of an 800 m² sample, extrapolating from smaller plot sizes when necessary. The placement and characteristics of the sample plots are summarized in Tables 3-2 and 3-3. Ten plots were established on slopes (P1–P10), and two were set up along watercourses (R1 and R2).

Ecological Sampling

Each plot (measuring 800 m², or in some cases only 700 or 300 m²), with the exception of those along watercourses, was subdivided into basic units of 100 m² to facilitate sampling and to allow for frequency calculations.

The following information was noted for each plot: (A) locality (latitude and longitude) and the date when the census was made; (B) altitude, topographic position, slope, and exposure; (C) general physiognomy of the vegetation (density and diameter of the trees; abundance of mosses, lichens, and other epiphytes; abundance of lianas, etc.); (D) number and approximate height of the woody and herbaceous layers; (E) cover (%) of each layer, using Folk (1951; cf. also Godron et al., 1983, p. 163); (F) thickness of the litter layer; (G) thickness and color of the humus; and (H) thickness and color of the soil, or the upper layer of soil when total thickness exceeded 30 cm.

The following floristic observations were noted in each 100 m² base unit within the plots. (A) An exhaustive list of the species present was made. (B) The number of individuals or colonies of each species was determined and scored according to the following abundance classes: 1, a single individual or colony; 2, 2–4 individuals or colonies; 3, 5–9 individuals or colonies; 4, 10–19 individuals or colonies; 5, 20–49 individuals or colonies; and 6, ≥50 individuals or colonies. For little epi-

phytic clonal species that cover a large unbroken area on trunk (Hymenophyllaceae, Grammitidaceae), each area unit of 400 cm^2 (20 × 20 cm) was arbitrarily considered one colony. For bigger, terrestrial or epiphytic, gemmiferous species (e.g., *Asplenium sandersonii, A. poolii*), individuals or colonies could easily be scored: all plants that remain in contact by their rooted rhachis form one colony. (C) The habit of each species (terrestrial, epiphytic, epilithic, or lianescent) was described. Because many primarily epiphytic ferns can also grow on rocks and because terrestrial species can do likewise (although less frequently), the following categories of species were recognized: terrestrial or more rarely epilithic, epiphytic or more rarely epilithic, strictly epilithic, lianescent, and terrestrial, epiphytic, or more rarely epilithic. Habit was defined using the following characters. Terrestrial and lianescent plants are rooted in the litter, humus, or soil. The vegetative parts of terrestrial plants are erect or scrambling; those of lianescent plants are erect and twisted around supporting structures (usually trees). Epiphytic plants grow on other plants (living or dead) and are not in contact with the soil. (The rhizomes of an epiphytic fern may be erect or scrambling; parasitic ferns do not exist.) Epilithic plants are attached to stones or rocks; in cases in which the substrate is covered with humus or moss, a plant is regarded as epilithic if the tips of its roots are in contact with the surface of the stone or rock (otherwise it is considered to be terrestrial).

Some ferns with elongated rhizomes, such as *Blechnum attenuatum* and *Lomariopsis crassifolia*, often referred to as hemiepiphytes, are terrestrial during their early stages of development or in particular ecological conditions and can then become epiphytic by growing onto a tree after their older parts degenerate. In these cases, the habit recorded was that exhibited by the plant on the date of sampling (terrestrial or epiphytic).

Observations of epiphytes in the forest canopy were made using binoculars. During the first phase of study at each plot, identification of these species was facilitated by making use of (a) steep terrain in which the canopy is closer to eye level, (b) large rocks along rivers or in the forest, (c) openings in the forest where heliophilous epiphytes normally found high in the canopy tend to grow closer to the ground, and (d) canopy trees that had recently fallen. Even with the use of these techniques, however, the number of epiphytic species recorded is likely underestimated.

Analysis of Data

The sampling layout used in the RS d'Anjanaharibe-Sud (Tables 3-2 and 3-3) was based on the hypothesis that altitudinal and topographic factors could influence the mode of distribution of pteridophytes within the study area, as we had observed in other Malagasy regions (Rakotondrainibe, 1989; Rakotondrainibe & Raharimalala, 1996). To test this hypothesis, the data obtained from the plots were treated using two classic and complementary types of multivariate analysis (using STATITCF, version 4): correspondence analysis (CA) (Legendre & Legendre, 1984a,b; Benzécri & Benzécri, 1984) and hierarchical ascending classification (HAC) (Jambu, 1978; Fenelon, 1981; Legendre & Legendre, 1984b).

The data matrix used for the analyses listed in rows all 175 species recorded in the plot studies (of 211 species listed in Table 3-1) against columns of each of the 12 plots sampled (P1–P10, R1, and R2). Each cell of the matrix contained the corresponding abundance code (1–6) as defined above. For the analysis, all elements in each column were active.

The two types of analyses used made it possible to visualize and to interpret the structures that occur within the body of data by χ^2 analysis of the relationships between the different elements of the matrix. Correspondence analysis yields a representation, in multidimensional space, of the plot and/or species points and reveals gradients among the data. Hierarchical ascending classification results in a tree or dendrogram comprising a hierarchical and progressive grouping of plot or species units in sets of increasing size. The criterion used here for grouping units into a class is the average of the weighted distances.

Results

Overall Floristic Analysis

SPECIES RICHNESS—A total of 211 pteridophyte species or infraspecific taxa in 60 genera were recorded between 600 and 2000 m elevation on the east and southeast slopes of the RS d'Anjanaharibe-Sud Massif (Fig. 3-1). A list of these taxa is provided in Table 3-1. The genera with the largest number of species are *Asplenium* (23 species and three varieties), *Elaphoglossum*

(21 species), *Cyathea* (17 species), *Hymenophyllum* (14 species), *Trichomanes* (13 species), *Huperzia* (9 species), *Blechnum* (7 species and 2 varieties), *Ctenopteris* (9 species), and *Grammitis* (9 species).

HABIT—The percentages of the various habit types represented in Figure 3-2 were calculated from the data in Table 3-1. More than half of the taxa (113, or 53.6%) are epiphytic or more rarely epilithic 80 taxa (37.9%) are terrestrial or more rarely epilithic, and only 11 (5.2%) are terrestrial, epiphytic, or more rarely epilithic. Two taxa (0.9%), *Lygodium lanceolatum* and *Trichomanes speciosum*, are lianescent, and five taxa (2.4%), *Asplenium inaequilaterale*, *A. marojejyense*, *Elaphoglossum spathulatum*, *T. longilabiatum*, and *Vittaria scolopendrina*, were observed only on rocks (strictly epilithic).

NOTEWORTHY TAXA—The names of taxa endemic to Madagascar appear in boldface type in Table 3-1. There are 82 such taxa in all, representing 38.9% of the pteridophyte flora of the massif.

Five species are considered endemic to the Anjanaharibe chain on the basis of available data. *Diplazium andapense* was collected earlier, in 1950, by Humbert on the slopes of Anjanaharibe-Nord Massif, between 1200 and 1600 m altitude, and was found again during the present study on the southeast slope of the RS d'Anjanaharibe-Sud, once at 1270 m and several times between 1550 and 1650 m. This species can easily be confused with *D. zakamenense*, which is common in Madagascar, but *D. andapense* differs in the subcoriaceous texture of its fronds and the presence of black scales on all its axes (Tardieu-Blot, 1955).

Four new taxa were collected during the field work for the present study. These include *Blechnum* sp. nov., *ined.* (FR 2384); *Cyathea* sp. nov., *ined.* (FR 2524); *Elaphoglossum* sp. nov., *ined.* (FR 2270, 2469, and 2480); and *Grammitis* sp. nov., *ined.* (FR 2500 and 2526).

Two nonendemic species are known in Madagascar only from the Anjanaharibe chain. *Ctenopteris torulosa*, which is common in Réunion (F. Badré, pers. comm.), has been recorded in Madagascar from only two stations located at about 1600 m, one on the slopes of Anjanaharibe-Nord and the other on the RS d'Anjanaharibe-Sud. *Xiphopteris sikkimensis*, an Asian species, is recorded here for the first time in Madagascar in high abundance in ridge forest near the summit of the RS d'Anjanaharibe-Sud, between 1950 and 2000 m.

Five taxa collected within the reserve make up important new distributional records for Madagascar: *Grammitis obtusa*, previously collected by Pervillé on Nosy Be; *Huperzia gagnepainiana*, whose holotype (Perrier de la Bâthie 15405, P) was collected on the Tsaratanana Massif; *Lastreopsis subsimilis*, collected only once in Madagascar by Goudot, with no indication of the exact locality; *Hymenophyllum polyanthos* var. *kuhnii*, recorded for the first time in Madagascar on the Andringitra Massif (Rakotondrainibe & Raharimalala, 1996); and *Elaphoglossum marojejyense*, previously collected only on the Marojejy Massif.

Seven species whose previously known distribution in Madagascar was limited to the extreme north of the island were observed in the RS d'Anjanaharibe-Sud, confirming the floristic richness and the floristic originality of the region: *Blechnum madagascariense* (Réserve Naturelle Intégrale (RNI) du Marojejy, eastern slope of Marojejy Massif and Mount Beondroka); *Blechnum* sp. nov., *ined.* (Rakotondrainibe 2548) (RNI du Marojejy and near Baie d'Antongil); *Asplenium marojejyense* and *Ctenopteris alboglandulosa* (Marojejy and Manongarivo massifs); *Didymochlaena microphylla* (Manongarivo, Tsaratanana, and Marojejy massifs); *Lindsaea blotiana* (Manongarivo and Marojejy massifs, Masoala Peninsula); *Cyathea auriculata* (Marojejy Massif and Masoala Peninsula); and *Grammitis copelandii* (Réserve Intégrale du Marojejy, eastern slope of Marojejy Massif and Mount Beondroka and south of Vohémar).

Two localized Malagasy endemic species collected by Humbert in the north of the Anjanaharibe Massif were not found in the RS d'Anjanaharibe-Sud, *Lindsaea humbertii* (Tardieu) Kramer and *Lonchitis coriacea* Tardieu.

DISTRIBUTION OF TAXA—Statistical analysis of the plot samples shows (Figs. 3-2–3-7) that a strong altitudinal gradient exists within the pteridophyte flora of the south and southeast slopes of the RS d'Anjanaharibe-Sud Massif, compounded at low altitude by a topographic gradient. Analysis of the floristic composition of each altitudinal stage is based on both the statistical results explained below and the information presented in Table 3-1.

Altitudinal and Topographic Gradients—Figures 3-3 and 3-4 indicate the positions of plots P1–P10, R1, and R2 on axes I and II (Fig. 3-3) and axes I and III (Fig. 3-4) of the correspondence analysis. For clarity, only structuring species, that is, those that contribute substantially ($\geq 1.8\%$) to
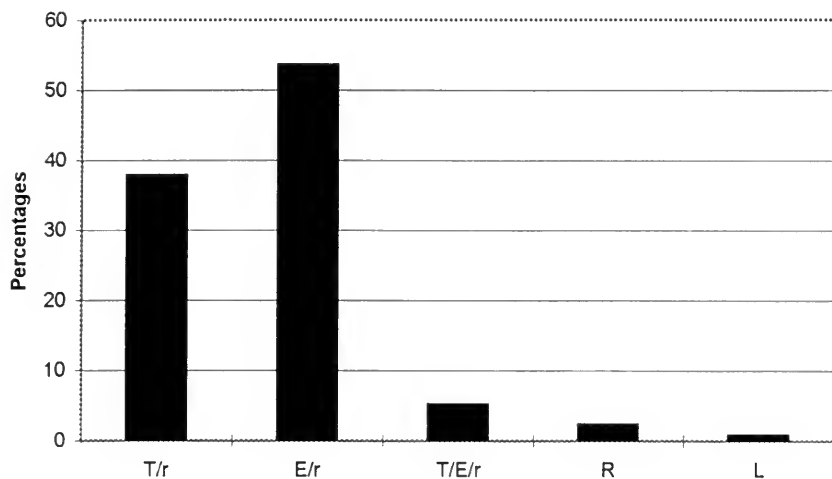
FIG. 3-2. Percentages of the whole pteridophyte flora (211 species listed in Table 3-1) by habit type in the RS d'Anjanaharibe-Sud. T/r-terrestrial or more rarely epilithic species; E/r-epiphytic or more rarely epilithic species; R-strictly epilithic species; L-lianescent species and T/E/r-terrestrial, epiphytic, or more rarely epilithic species.

the inertia of one or the other of the factorial axes, have been shown. The species numbers in the figures correspond to those indicated in Table 3-1. The five clusters of plots distinguished by dividing the hierarchical tree in Figure 3-5 between nodes 19 and 20 serve to delimit the cloud of plot points in the CA diagrams.

In the diagram of axes I and II from the CA (Fig. 3-3), the plots form a parabolic curve (Guttman effect), which indicates a strong gradient within the data. Axes I and II express the same altitudinal gradient: axis I separates, on the positive side, plots R1, P1, P2, and P3, which occur at low altitude (800–1000 m), and, on the negative side or near the origin of the axis, plots R2 and P4–P10, located at middle to higher elevations (1250–2000 m), axis II separates plots P4–P8 and R2, occurring at middle elevations (1250–1650 m), from plots P9 and P10, located near the summit (1900–2000 m).

The projections of points on axes I–IV and I–V are not shown, but dividing the HAC tree between nodes 16 and 17 indicates clear floristic differences between (P7, P8) and (P9, P10) on one hand and between (P4, P5, P6) and (P7, P8) on

the other. The values of the absolute contributions to inertia of axes IV and V of the structuring species are indicated in Table 3-6.

Altitudinal gradient explains most of the floristic heterogeneity among the plots. On the basis of the floristic composition of the pteridophytes, three altitudinal zones can be recognized on the south-southeast slope of the RS d'Anjanaharibe-Sud.

1. *A lower zone, up to 1020 m*. We suspect that quantitative data from plots between 600 and 700 m would probably show the lower zone to be divided into two subzones, one at about 600–700 m and the other at around 820–1020 m (sample plots P1, P2, P3, and R1). Floristic differences between these two subzones can be noted in Table 3-1. *Asplenium marojejyense* and *Bolbitis auriculata* are frequent at about 600–700 m and absent at around 820–1020 m; many species that are frequent at around 820–1020 m are absent or rare at about 600–700 m.

2. *A middle-altitude zone, between 1250 and 1650 m*. This zone can be divided into two subzones, one at around 1220–1350 m (P4, P5, P6, R2) and the other toward 1550–1650 m (P7, P8).

←

FIG. 3-1. Examples of the rich pteridophyte flora of the RS d'Anjanaharibe-Sud. Top row, left to right: *Cyathea decrescens* Mett., a relatively frequent tree-fern, usually occurring along streams or on lower slopes between 820 and 1350 m, and *Cyathea costularis* Bonap., a tree-fern restricted to shaded ravines or near streams between 1550 and 1650 m. Bottom row, left to right: *Ctenopteris devoluta* (Baker) Tardieu, an epiphyte growing at middle and lower levels of the canopy between 1250 and 1650 m, and *Elaphoglossum decaryanum* Tardieu, a rare epiphyte found in the middle level of the canopy between 1250 and 1650 m. (Photographs by F. Rakotondrainibe.)
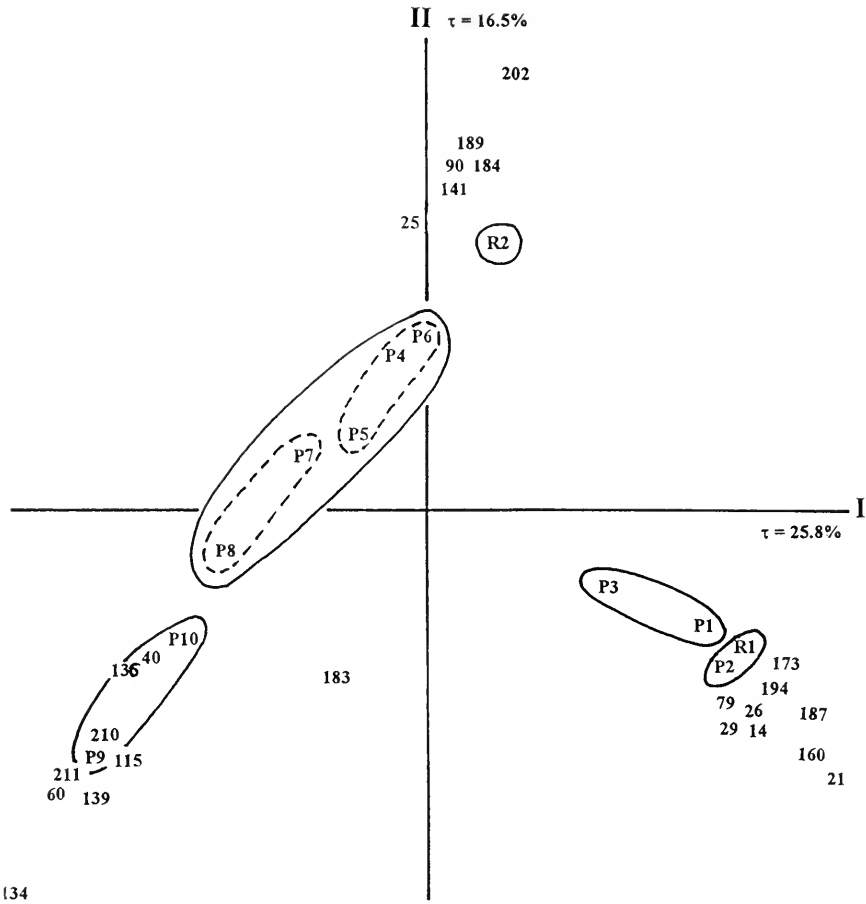
FIG. 3-3. Correspondence analysis of the matrix of 12 plots and 175 pteridophyte species: projection on axes I and II of all plots (P1–P10, R1, and R2) and the species that contribute at least 1.8% to the inertia of one or the other of the factorial axes. Species numbers are those given in Table 3-1.

3. *An upper zone, between 1900 and 2000 m (P9, P10).* Without taking samples along a continuous altitudinal gradient, it is not possible to determine the precise limits of the boundaries between one zone or subzone and the next.

On the projection of axes I and III of the CA (Fig. 3-4), the cluster of plots located at low altitude extends along axis III and is broken into topographic subunits: R1 along a stream, P2 on a lower slope, P1 on a middle slope, and P3 on a ridge. Between 1250 and 1350 m, the samples from watercourses (R2) and lower slopes (P6) are clearly separated along the same axis, whereas the plots from the middle slope (P5) and the ridge (P4) remain grouped together, as is also indicated by the projection of these points on axes II and III (not shown). The same holds true for the plots from the middle slope (P7) and the ridge (P8) at

1570–1600 m and for the plots from the middle slope (P10) and the ridge (P9) at 1900–2000 m, near the summit. Thus, at low altitude there is a strong topographic gradient that diminishes as one approaches the summit.

Floristic Analysis of Each Altitudinal Zone— Habit Types (Fig. 3-6, Table 3-4): The percentage of pteridophyte species belonging to the various habit types changes as a function of atmospheric humidity and soil characteristics. Between 600 and 700 m, 42.3% of the species are terrestrial or rarely epilithic. Because of the presence of numerous boulders, strictly epilithic species are also frequent (30.8%). Starting at 820 m, atmospheric humidity increases substantially, and epiphytic species become dominant; their percentage reaches its maximum value (65.7%) at 1550–1650 m. At 2000 m, on the ridge, mosses make up a dense,

FIG. 3-4. Correspondence analysis of the matrix of 12 plots and 175 pteridophytes species: projection on axes I and III of all plots (P1–P10, R1, and R2) and the species that contribute at least to 1.8% to the inertia of one or the other of the factorial axes. Species numbers are those given in Table 3-1.

FIG. 3-5. Hierarchical ascending classification tree using a cross matrix of 12 plots (P1–P10, R1, and R2) and 175 species of pteridophytes. The criterion used for grouping units into a class is the average of the weighted distances.

Fig. 3-6. Percentages of the pteridophyte flora (211 species listed in Table 3-1) by habit type for each altitudinal zone in the RS d'Anjanaharibe-Sud. T/r-terrestrial or more rarely epilithic species; E/r-epiphytic or more rarely epilithic species; R-strictly epilithic species; L-lianescent species; and T/E/r-terrestrial, epiphytic, or more rarely epilithic species.

nearly continuous cover and form a very thick mat around trunks and large branches; individuals of many species are thus indifferently terrestrial or epiphytic. The percentages of the various habit types on the ridge are distributed as follows: 44.1% epiphytes or more rared epilithic; 41.2% terrestrial, epiphytic, or epilithic; and 14.7% always terrestrial or more rarely epilithic.

Floristic Richness at the Generic Level (Fig. 3-7): Because fern genera for the most part have wide paleo- or pantropical geographic distributions, data from pteridological inventories are generally expressed at the species rather than the generic level. However, as the results presented below indicate, it can be useful in certain cases, especially those involving ecological considerations, to assess patterns of richness at the generic level as well.

TABLE 3-4. Pteridophyte habit for each altitudinal zone.

Habit type*	Coverage (%)					
	600–700 m	820–1020 m	1250–1350 m	1550–1650 m	1990–1990 m	2000 m (ridge)
T/r	42.3	34.8	37.7	32.4	29.5	14.7
E/r	23.1	59.8	55.7	65.7	62.3	44.1
T/E/r	1.9	2.7	2.5	1.9	6.6	41.2
R	30.8	0.9	3.3	0	1.6	0
L	1.9	1.8	0.8	0	0	0

* T/r = terrestrial or more rarely epilithic species; E/r = epiphytic or more rarely epilithic species; R = strictly epilithic species; L = lianescent species; T/E/r = terrestrial, epiphytic, or more rarely epilithic species.

The distribution of floristic richness at the generic level within the RS d'Anjanaharibe-Sud appears to be nonrandom. Between 600 and 700 m, the fern flora is represented by 29 genera; between 820 and 1020 m, by 43 genera; between 1250 and 1350 m, by 39 genera; between 1550 and 1650 m, by 35 genera; and near the summit, between 1900 and 2000 m, by 20 genera. This variation in generic richness within the fern flora is accompanied by a modification in the generic composition at the different altitudinal zones. Table 3-5 shows, for each zone, the specific richness of the nine largest (i.e., most speciose) genera of ferns occurring on the massif. The number of species in each of the nine genera is relatively small at low altitudes and near the summit. Furthermore, between 820 and 1650 m, the flora becomes progressively less rich in species belonging to the genera *Asplenium* and *Trichomanes* but increases in members of the genera *Elaphoglossum*, *Huperzia*, *Ctenopteris*, and *Grammitis*. Diversity within the genera *Hymenophyllum* and *Blechnum* is highest between 1250 and 1350 m; that of *Cyathea* remains more or less constant between 820 and 1650 m.

Floristic Richness at the Species Level (Fig. 3-7): Species richness also varies with altitude: 52 species occur between 600 and 700 m; 112 species occur between 820 and 1020 m, 122 species occur between 1250 and 1350 m, 105 species occur between 1550 and 1650 m; and 61 species occur between 1900 and 2000 m.

The floristic list of species observed within each elevational zone is given in Table 3-1. In
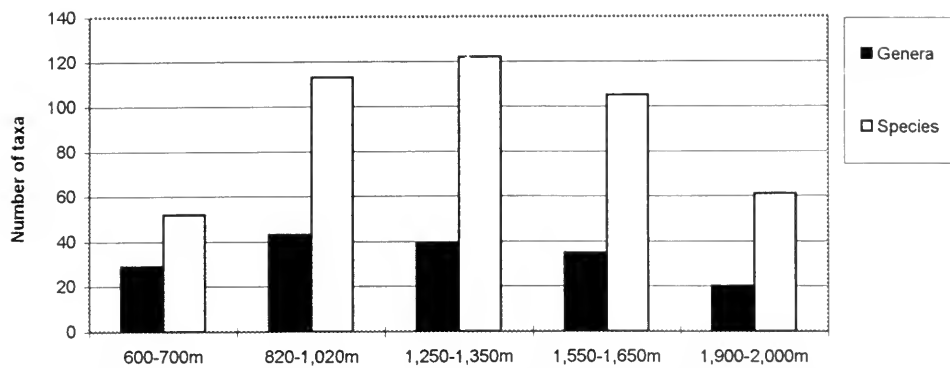
FIG. 3-7. Generic and specific floristic richness of all pteridophytes (211 species listed in Table 3-1) in each altitudinal zone in the RS d'Anjanaharibe-Sud.

attempting to define the ecological status of each species, we relied on the data from this overall inventory and on the results of the statistical analyses of the samples, summarized in Figures 3-3 and 3-4 and Table 3-6. Because ecological conclusions cannot be reached on the basis of the presence of rare or infrequent species (69 taxa in all), we discuss only those that are frequent and/or abundant. Adopting the terminology widely used by phytosociologists (Braun-Blanquet, 1964, Guinochet, 1973), a species is regarded as an "exclusive characteristic" of an altitudinal zone if its distribution is limited strictly to that zone. The notion of structuring species, in the context of the statistical analyses of the samples, implies the idea of a preferential but nonexclusive presence of these species in some of these samples, which results in high coefficients of abundance; these structuring species are referred to as "preferential species." It should be noted that the status of exclusive characteristic or preferential species in an altitudinal zone is applied here to a very limited region (the south-southeast slope of the RS

d'Anjanaharibe-Sud) and thus is not equivalent to the more general notion used in phytosociology.

A relatively low number of species that are tolerant of local conditions have wide distributions that extend over all, or nearly all, of the slope (Table 3-1). These species are mostly widespread in Madagascar:

15 *Asplenium cancellatum*
20 *Asplenium herpetopteris* var. *herpetopteris*
18 *Asplenium herpetopteris* var. *massoulae*
37 *Blechnum attenuatum*
46 *Blotiella madagascariensis*
58 *Ctenopteris devoluta*
63 *Ctenopteris villosissima*
65 *Cyathea* aff. *hildebrandtii*
75 *Cyathea hildebrandtii*
88 *Diplazium zakamenense*
100 *Elaphoglossum deckenii* var. *rufidulum*
101 *Elaphoglossum humbertii*
111 *Elaphoglossum subsessile*
135 *Hymenophyllum capense*

TABLE 3-5. The number of species documented in each altitudinal zone of the nine largest pteridophyte genera.

Genus	600–700 m	820–1020 m	1250–1350 m	1550–1650 m	1900–2000 m	Total 600–2000 m
Asplenium	9	17	16	9	4	26
Trichomanes	4	11	11	7	2	13
Elaphoglossum	2	11	14	14	9	21
Huperzia	1	2	4	6	3	9
Ctenopteris	2	4	4	8	5	9
Grammitis	0	1	5	7	6	8
Hymenophyllum	0	4	12	10	9	14
Blechnum	1	4	7	3	3	9
Cyathea	3	9	8	10	6	15

TABLE 3-6. List of structuring species,* value (%) of their contribution to the inertia of the first five factorial axes, and their position on these axes.

No.	Taxon	Axis I	II	III	IV	V
7	*Arthropteris orientalis*			2.3 (+)		
10	*Asplenium* aff. *anisophyllum*			3.0 (+)		
14	*Asplenium bipartitum*	2.0 (+)				
17	*Asplenium friesorum*					3.1 (+)
19	*Asplenium herpetopteris* var. *acutipinnata*					2.0 (+)
21	*Asplenium herpetopteris* var. *villosum*	1.8 (+)		1.9 (−)		
22	*Asplenium inaequilaterale*			2.0 (−)		
26	*Asplenium nidus*	2.7 (+)				
29	*Asplenium pellucidum*	1.9 (+)				
33	*Asplenium unilaterale*			1.8 (−)		
37	*Blechnum attenuatum*					3.7 (+)
40	*Blechnum madagascariense*	2.0 (−)				
57	*Ctenopteris deltodon*				2.4 (+)	
64	*Ctenopteris zenkeri*			2.0 (+)		
60	*Ctenopteris flabelliformis*	1.8 (−)	2.1 (−)		2.4 (−)	
66	*Cyathea* aff. *simliis*					2.4 (−)
72	*Cyathea coursii*				3.7 (+)	2.3 (−)
74	*Cyathea dregei* var. *polyphlebia*					2.3 (+)
79	*Cyathea serratifolia*	2.2 (+)		1.9 (+)		
86	*Diplazium andapense*				2.3 (+)	
88	*Diplazium zakamenense*			1.8 (−)		
90	*Dryopteris mangindranensis*		1.8 (+)			
91	*Dryopteris remotipinnula*				1.9 (−)	
98	*Elaphoglossum coriaceum*			3.5 (+)		
104	*Elaphoglossum leucolepis*					3.8 (+)
106	*Elaphoglossum petiolatum* ssp. *salicifolium*				2.3 (+)	
111	*Elaphoglossum subsessile*			3.6 (+)		
112	*Elaphoglossum welwitschii*				3.3 (+)	2.0 (−)
115	*Grammitis copelandii*	1.9 (−)	1.9 (−)			
117	*Grammitis gilpinae*				3.0 (+)	
120	*Grammitis obtusa*				4.1 (+)	2.5 (−)
134	*Hymenophyllum* aff. *ivohibense*		1.8 (−)		2.4 (−)	
136	*Hymenophyllum capillare*	1.9 (−)				
139	*Hymenophyllum humbertii*			1.9 (−)	2.8 (−)	
141	*Hymenophyllum perrieri*		2.0 (+)			
149	*Lastreopsis boivinii*				3.1 (+)	2.0 (−)
154	*Lindsaea madagascariensis*			2.1 (+)		
157	*Lygodium lanceolatum*			3.5 (+)		
160	*Microlepia madagascariensis*	2.0 (+)		1.9 (−)		
173	*Pneumatopteris subpennigera*	2.0 (+)		2.6 (−)		
176	*Pteris catoptera*			1.9 (−)		
183	*Rumohra adiantiformis*		2.0 (−)			
184	*Rumohra lokohoensis*		2.3 (+)			
186	*Schizaea dichotoma*				4.8 (+)	
187	*Selaginella fissidentoides*	3.0 (+)				
188	*Selaginella pectinata*				1.8 (+)	
189	*Selaginella unilateralis*		2.3 (+)			
192	*Trichomanes* aff. *cupressoides*					2.2 (−)
194	*Trichomanes bipunctatum*	2.9 (+)				
202	*Trichomanes meifolium*					2.1 (−)
210	*Xiphopteris oosora* var. *micropecten*	2.0 (−)	1.8 (−)			
211	*Xiphopteris sikkimensis*		1.9 (−)		2.3 (−)	

* Structuring species are species that contribute at least to 1.8% to the inertia of one or the other of the factorial axes.

† + = positive side; and − = negative side.

138 *Hymenophyllum hirsutum*
142 *Hymenophyllum polyanthos*
145 *Hymenophyllum sibthorpioides*
165 *Oleandra distenta*
169 *Pleopeltis excavata*
183 *Rumohra adiantiformis*
193 *Trichomanes* aff. *rigidum*
196 *Trichomanes borbonicum*

Two of these species, however, should be mentioned because each occurs preferentially in a well-determined biotope, as indicated by their position in the diagram of axes I and III in the CA (Fig. 3-4) and the value of their contribution to the inertia of axis III (Table 3-6): (88) *Diplazium zakamenense*, a preferential species of stream banks, and (111) *Elaphoglossum subsessile*, a preferential species of ridges.

Altitude, and in certain cases topography, determines the range of distribution for the majority of the other species.

Lower altitudinal zone (600–1020 m): 600–700 m—Exclusive characteristic species: (24) *Asplenium marojejyense*, (34) *Asplenium variabile* var. *paucijugum*, and (47) *Bolbitis auriculata*. 820–1.020 m—Exclusive characteristic species: (89) *Drynaria wildenowii* and (168) *Platycerium madagascariense*, both canopy epiphytes; (187) *Selaginella fissidentoides*, often forming dense carpets on the ground; (21) *Asplenium herpetopteris* var. *villosum*; and (176) *Pteris catoptera*, always localized on the lower slopes or along streams (see Table 3-6 for the value of their inertia in axis III). Preferential species: (173) *Pneumatopteris subpennigera*, which prefers both an altitudinal range (820–1020 m) and a topographic zone (lower slopes and stream banks). 600–1020 m—Exclusive characteristic species: (7) *Arthropteris orientalis* and (10) *Asplenium* aff. *anisophyllum*, which also shows a preference for ridges; (79) *Cyathea serratifolia* and (157) *Lygodium lanceolatum*, which prefer middle slopes; (160) *Microlepia madagascariensis* and (22) *Asplenium inaequilaterale*, which prefer lower slopes and stream banks; (14) *Asplenium bipartitum*; (16) *Asplenium cuneatum*; (29) *Asplenium pellucidum*; (82) *Davallia chaerophylloides*; (87) *Diplazium proliferum*; (161) *Microsorum punctatum*; (163) *Nephrolepis biserrata*; (166) *Phymatosorus scolopendria*; (172) *Pneumatopteris remotipinna*; (177) *Pteris elongatiloba* var. *remotivenia*; (181) *Pteris woodwardioides*; and (194) *Trichomanes bipunctatum*. Preferential species: (26) *Asplenium nidus*.

Middle altitudinal zone (1250–1650 m): 1250–1350 m—Exclusive characteristic species: (39) *Blechnum ivohibense*, (85) *Didymochlaena microphylla*, (153) *Lindsaea goudotiana*, (189) *Selaginella unilateralis*, (202) *Trichomanes meifolium*, and (184) *Rumohra lokohoensis*. Two heliophilous species, (123) *Histiopteris incisa* and (148) *Hypolepis sparsisora*, belong exclusively to this altitudinal zone but were observed only in clearings around old quarries; their inclusion in this group is thus perhaps not directly linked to altitudinal factors. 1550–1650 m—Exclusive characteristic species: (71) *Cyathea costularis*, (112) *Elaphoglossum* aff. *welwitschii*, (72) *Cyathea coursii*, (149) *Lastreopsis boivinii*, and (174) *Pseudocyclosorus pulcher*. Preferential species: (86) *Diplazium andapense*. 1250–1650 m—Exclusive characteristic species: (17) *Asplenium friesiorum*, (25) *Asplenium monanthes*, (51) *Coniogramme madagascariensis*, (86) *Diplazium andapense*, (117) *Grammitis gilpinae*, (136) *Hymenophyllum capillare*, (141) *H. perrieri*, and (175) *Pseudophegopteris cruciata*. Preferential species: (154) *Lindsaea madagascariensis*, which prefers both an altitudinal zone (1250–1650 m) and a topographic zone (middle slopes and ridges).

Upper altitudinal zone (1900–2000 m): Exclusive characteristic species: (61) *Ctenopteris humbertii*, (91) *Dryopteris remotipinnula*, and (134) *Hymenophyllum* aff. *ivohibense*. Preferential species: (139) *Hymenophyllum humbertii* and (211) *Xiphopteris sikkimensis*.

Discussion and Conclusions

When the results presented above are compared with those of inventories of the same type conducted in the last few years in several other protected areas in Madagascar, it is clear that the RS d'Anjanaharibe-Sud, with its 211 species and varieties of pteridophytes, has by far the richest pteridophyte flora of any area studied to date. A total of 188 species and varieties were observed in the Réserve Naturelle Intégrale d'Andringitra (Rakotondrainibe & Raharimalala, 1996), 169 in the RS de Manongarivo (Rakotondrainibe & Quansah, 1994), 157 in the Parc National (PN) de la Montagne d'Ambre (Rakotondrainibe & Rabelaza, unpubl. data), 155 in the PN de Ranomafana (Rahajasoa, 1993); and 155 in the RS d'Ambohitantely (Rakotondrainibe, 1989). These figures take into account only recent collections and in some cases

are based on inventory work that was less detailed than that carried out in the RS d'Anjanaharibe-Sud. The number of species needs to be verified against data from the literature and older collections. Nevertheless, these data indicate that the species-level richness of the pteridophyte flora of the RS d'Anjanaharibe-Sud is exceptional and that this protected area should be given special attention by those responsible for conservation projects.

The richness of the fern flora occurring in the reserve can be explained by the geographic position of the massif within one of the wettest areas of Madagascar (Donque, 1975; Chaperon et al., 1993) and by the fact that moist evergreen forest covers a wide altitudinal range, from 600 to 2064 m. Despite evidence of human impact, which is limited but definitely present and can be seen at lower altitudes between 600 and 1020 m along a few trails connecting isolated villages, and between 1250 and 1350 m in old quarries, the floristic diversity does not appear to have been substantially affected by anthropogenic forces.

The Marojejy Massif, which is located about 70 km northeast of the RS d'Anjanaharibe-Sud Massif and reaches 2133 m, might be expected to have as high a floristic diversity as found in the present study. However, Humbert, during his last two trips to Madagascar, recorded only 107 species of pteridophytes on Marojejy (Tardieu-Blot, 1955). It would be valuable to undertake new inventory work in this interesting zone to assess the pteridophyte diversity of Marojejy in a more rigorous way.

The Masoala Peninsula is also situated in this same climatic region, but the area has substantially less relief, with the highest point at 1105 m. The overall richness of the fern flora of Masoala is much lower than that of the RS d'Anjanaharibe-Sud (116 species and varieties, compared with 211). However, if one compares the number of taxa observed within the same altitudinal levels that occur in both areas (i.e., those between 600 and 1020 m), the pteridophyte species richness appears to be approximately the same. In fact, the results obtained from similar lengths of time devoted to exploration (10–11 days) using a comparable methodology show 119 taxa (species and varieties) from the Masoala Peninsula and 122 from the RS d'Anjanaharibe-Sud. These figures confirm that within a climatic region, altitudinal factors play an important role in the distribution of pteridophytes.

The particularly rich flora of the RS d'Anjanaharibe-Sud is also highly distinctive. Five fern species, four of which are new to science, are currently considered to be endemic to the massif, six additional species are known on Madagascar only from the massif, although they also occur in areas outside of Madagascar and thus are not endemic to the island.

Altitude is the factor that best explains the patterns of distribution of the pteridophyte taxa on the south-southwest slope of the RS d'Anjanaharibe-Sud. Histograms of species richness as a function of altitude (Fig. 3-7) show a regular bell curve with a maximal value near 1300 m, with each altitudinal zone having a substantial number of exclusive characteristic species. Pteridophytes are very sensitive to variations in certain ecological parameters, in particular atmospheric humidity, rainfall, and, to a lesser degree, light levels (Rakotondrainibe & Guillerm, 1990; Dzwonko & Kornas, 1994). Moreover, it is well known, notably on Madagascar, that the values of these parameters change more or less progressively with altitude on the windward slopes of massifs (Koechlin et al., 1974; Donque, 1975). On the southeast slope of the RS d'Anjanaharibe-Sud, despite the lack of precise meteorological data, one can safely assume that when the moist trade winds encounter the relief, they are uplifted in the same manner as elsewhere along Madagascar's eastern escarpment (Donque, 1975), resulting in the development of dense clouds above about 600–800 m, depending on the season, that produce orographic precipitation and fog banks. The shift in climate at this altitude is reflected by changes in the physiognomy of the vegetation and delimits the transition from lowland to midaltitude dense evergreen forest (Humbert, 1965; Koechlin et al., 1974). Epiphytic species (e.g., ferns, orchids, Crassulaceae, Piperaceae) are more frequent, and overall pteridophyte diversity increases. Starting at about 1500–1600 m, the physiognomy of the forest changes again; the number of woody strata and associated ecological niches decreases, and the canopy is lower and less dense (Table 3-2). In clear weather the sun penetrates more into the understory, and the pteridophyte flora shifts and becomes less rich. On the highest ridges intense sun during part of the day temporarily dries out the atmosphere, which prevents the growth of numerous pteridophyte species that are sensitive to sharp daily fluctuations in light intensity and atmospheric humidity levels. This model of the altitudinal distribution of diversity, with comparatively few species at low elevations and near the

summits and maximum diversity at middle altitudes, has been described often for ferns in various parts of the world (Jacobsen & Jacobsen, 1989; Young & Leon, 1991; Parris et al., 1992) but may not apply as a general rule for angiosperms (Gentry, 1988).

The percentages of the different habit types in each pteridophyte altitudinal zone are influenced by a larger number of factors. Thus, the histogram of habit types for each altitudinal level is less regular (Fig. 3-6). At 600–700 m, terrestrial and epilithic ferns are more numerous, resulting most likely from comparatively lower atmospheric humidity and also from the presence of a greater number of boulders (at least within the study area). Starting at 820 m and extending almost to the summit, epiphytic ferns are clearly dominant. However, from 1250–1350 m, heliophilous, terrestrial species appear in the areas around old quarries, resulting in a substantially reduced proportion of epiphytes as compared to the altitudinal zones above and below this zone.

At low altitudes the floristic composition also varies across the slopes. Three distinct communities of pteridophytes can be characterized: one along watercourses, another on lower slopes, and a third on ridges. This humidity gradient, which is linked to topography, decreases progressively at higher altitudes, that is, as the atmosphere becomes saturated with water vapor, thus compensating for the water deficit in the well-drained soils. As a result, above 1500 m the forest ecosystem becomes more simple, with a decrease in the number of ecological niches and a reduction in biological diversity.

New Pteridophyte Records for Madagascar

Hymenophyllum polyanthos (Sw.) Sw. var. *kuhnii* (C.Chr.) Schelpe

Xiphopteris sikkimensis (Hieron.) Copel.

New Combinations

Diplazium andapense **(Tardieu) Rakotondrainibe comb. nov.**

Athyrium andapense Tardieu, Bull. Mus. Natl. Hist. Nat., sér, 2, **29:** 291 (1957). Type: Madagascar, Humbert 24614 (holotype P!).

Cyathea coursii **(Tardieu) Rakotondrainibe comb. nov.**

Alsophila coursii Tardieu, Bull. Soc. Bot. France, **258:** 684 (1941). Type: Madagascar, Humbert & Cours 17861 (holotype P!).

Acknowledgments

Literature Cited

BENZÉCRI, J. P., AND F. BENZÉCRI. 1984. Pratique de l'analyse des données. 1. Analyse des correspondances, exposé élémentaire, 2nd ed. Bordas, Paris, 456 pp.

BRAUN-BLANQUET, J. 1964. Pflanzensoziologie. *In* Grundzüge der Vegetationskunde, 3rd ed. Springer, Wien, New York, 865 pp.

BURROWS, J. E. 1990. Southern African ferns and fern allies. Frandsen Publishing, Sandton, 359 pp.

CHAPERON, P., J. DANLOUX, AND L. FERRY. 1993. Fleuves et rivières de Madagascar. Editions Orstom, Montpellier, 874 pp.

DONQUE, G. 1975. Contribution Géographique à l'Étude du Climat de Madagascar. Nouvelle Imprimerie des Arts Graphiques, Antananarino Madagascar, 477 pp.

DUVIGNEAUD, G. 1955. Etudes écologiques de la végétation en Afrique tropicale: Les divisions écologiques du monde. Année Biologique, Sér. 3, **31:** 375–392.

DUVIGNEAUD, G. 1980. La synthèse écologique: populations, communautés, écosystèmes, biosphère, 2nd ed. Doin, Paris, 380 pp.

DZWONKO, Z. AND J. KORNAS. 1994. Patterns of species richness and distribution of pteridophytes in Rwanda (Central Africa): A numerical approach. Journal of Biogeography, **21:** 491–501.

FENELON, J. P. 1981. Qu'est-ce que l'Analyse des Données? Lefonen, Paris, 311 pp.

FOLK, L. 1951. A comparison chart for visual percentage estimation. Journal of Sedimentary Petrology, **21**(1): 32–33.

GENTRY, A. H. 1988. Change in plant community and floristic composition on environmental and geographical gradients. Annals of the Missouri Botanical Garden, **75:** 1–34.

GODRON M., PH. DAGET, G. LONG, C. SAUVAGE, L. EMBERGER, E. LE FLOC'H, J. POISSONET, AND J. P. WAC-

QUANT. 1983. Code Pour le Relevé Méthodique de la Végétation et du Milieu. CNRS, Paris, 292 pp.

GUINOCHET, M. 1973. Phytosociologie. Editions Masson ed., Paris, 227 pp.

HOLTTUM, R. E. 1974. *Thelypteridaceae* of Africa and adjacent islands. Journal of South African Botany, **40**(2): 123–128.

HOLTTUM, R. E. 1981. The tree ferns of Africa. Kew Bulletin **36**:463–482.

HUMBERT, H. 1965. Description des types de végétation, pp. 46–78. *In* Humbert, H., and G. Cours-Darne, eds. Notice de la carte de Madagascar. Travaux de la Section Scientifique et Technique de l'Institut Français de Pondichery, hors séries, vol. 6.

JACOBSEN, W. B. G. AND N. H. G. JACOBSEN. 1989. Comparison of the pteridophyte flora of southern and eastern Africa, with special reference to high-altitude species. Bulletin du Jardin Botanique de Belgique, **59**: 261–317.

JAMBU, M. 1978. Classification Automatique pour l'Analyse des Données. 1. Méthodes et Algorithmes. Editions Bordas, Paris, 310 pp.

JOHNS, R. J. 1991. Pteridophytes of tropical East Africa: A Preliminary Check-list of the Species. Royal Botanic Gardens, Kew, England 131 pp.

KOECHLIN, J., J.-L. GUILLAUMET, AND P. MORAT. 1974. Flore et Végétation de Madagascar. J. Cramer Verlag, Vaduz, 687 pp.

KUBITZKI, K. 1990. The Families and Genera of Vascular Plants. Volume I: Pteridophytes and Gymnosperms. K. U. Kramer and P. S. Green, eds. Springer-Verlag, Berlin, 404 pp.

LEGENDRE, L. AND P. LEGENDRE. 1984a. Ecologie Numérique. 1. Le Traitement Multiple des Données Écologiques, 2nd ed. Editions Masson, Paris, and les Presses de l'Université Laval, Québec, 260 pp.

———. 1984b. Ecologie Numérique. 2. La Structure des Données Écologiques, 2nd ed. Editions Masson, Paris, and les Presses de l'Université Laval, Québec, 335 pp.

ØLLGAARD, B. 1989. Index of the *Lycopodiaceae*. Biologiske Skrifter, Kongelige Danske Videnskabernes Selskab, Copenhagen, **34**: 1–135.

PARRIS, B. S., R. S. BEAMAN, AND J. H. BEAMAN. 1992. The Plants of Mount Kinabalu 1. Ferns and Fern Allies. Royal Botanic Gardens, Kew, 165 pp.

PICHI-SERMOLLI, R. E. G. 1977. Tentamen Pteridophytorum genera in taxonomicum ordinen redigendi. Webbia, **31**(2): 313–512.

RAHAJASOA, G. 1993. Analyse de la diversité des Ptéridophytes dans le Parc National de Ranomafana. Diplôme d'Etudes Approfondies, Université d'Antananarivo, Madagascar.

RAKOTONDRAINIBE, F. 1989. Etude floristique, biologique, phytogéographique et écologique des fougères et plantes alliées de la forêt d'Ambohitantely (forêt tropicale d'altitude). Thèse de Doctorat, Université de Lille.

RAKOTONDRAINIBE, F. AND J. L. GUILLERM. 1990. Modèle de répartition horizontale des ptéridophytes le long d'un gradient d'humidité lié à la topographie: Le cas d'une forêt naturelle à Madagascar. Candollea, **45**: 591–598.

RAKOTONDRAINIBE, F. AND N. QUANSAH. 1994. The diversity and originality of the pteridophytes of the forest of Manongarivo Special Reserve (north-west Madagascar). Fern Gazette, **14**(7): 259–267.

RAKOTONDRAINIBE, F. AND F. RAHARIMALALA. 1996. The pteridophytes of the eastern slopes of the Réserve Naturelle d'Andringitra, Madagascar, pp. 76–82. In Goodman, S. M., ed. A floral and faunal inventory of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: With reference to elevational variation. Fieldiana: Zoology, n.s., **85**: 1–319.

RAKOTONDRAINIBE, F. AND F. RAHARIMALALA. In press. Contribution à l'étude de la flore des Aires Protégées de Madagascar: Les ptéridophytes de la presqu'île Masoala. Revue du Centre National de Recherche sur l'Environnement, Madagascar.

SCHELPE, E. A. C. L. E. 1990. Pteridophyta. *In* Exell, A. W., and E. Launert, eds. Flora Zambesiaca. Crown Agents, London, 254 pp.

TARDIEU-BLOT, M. L. 1951–1971. Les Ptéridophytes. *In* Humbert, H., ed., Flore de Madagascar et des Comores. Muséum National d'Histoire Naturelle, Paris.

TARDIEU-BLOT, M. L. 1955. Les fougères du massif du Marojejy. Mémoire de l'Institut Scientifique de Madagascar, Séries. B, **6**: 219–243.

VANDEN BERGHEN, C. 1973. Initiation à l'Étude de la Végétation, 2nd ed. Les Naturalistes Belges, Bruxelles, 236 pp.

YOUNG, K. R. AND B. LEON. 1991. Diversity, ecology and distribution of height-elevation pteridophytes within Rio Abiseo National Park, north-central Peru. Fern Gazette, **14**(1): 25–39.

Chapter 4

Ant Diversity Patterns Along an Elevational Gradient in the Réserve Spéciale d'Anjanaharibe-Sud and on the Western Masoala Peninsula, Madagascar

Brian L. Fisher[1]

Abstract

Leaf litter ant faunas were inventoried in Madagascar at 875, 1200, 1280, 1565, and 1985 m in the Réserve Spéciale (RS) d'Anjanaharibe-Sud and at 25, 425, and 825 m on the western Masoala Peninsula. Within each elevational zone, survey methods involved a combination of pitfall and leaf litter sampling along a 250 m transect. From pitfall and leaf litter samples, I collected and identified 24,586 ants belonging to 180 species and 25 genera in the RS d'Anjanaharibe-Sud; general collecting yielded an additional 35 species. On the Masoala Peninsula, pitfall and leaf litter collections yielded 52,307 ants comprising 167 species and 25 genera; general collecting added 30 more species. For the RS d'Anjanaharibe-Sud and the Masoala Peninsula combined, a total of 325 species and 34 genera were collected.

For each elevation, two different species richness estimators, incidence-based coverage estimator and first-order jackknife, gave comparable results. Species accumulation curves approached an asymptote and demonstrated the efficacy of these inventory techniques. Species collected and their relative abundances are presented. Species richness peaked at midelevation. Species turnover and faunal similarity measures demonstrated a division in ant communities between lowland forest ≤875 m and montane forest ≥1200 m. A midelevation peak in species richness is argued to be the result of the mixing of two distinct, lower and montane forest ant assemblages.

Résumé

L'entomofaune des fourmis de la litière du sol de la Réserve Spéciale d'Anjanaharibe-Sud a été inventoriée à 875, 1200, 1280, 1565, et 1985 m d'altitude ainsi qu'à 25, 425, et 825 m d'altitude dans la partie occidentale la péninsule de Masoala. Au niveau de chaque station altitudinale échantillonnée, les méthodes d'inventaire utilisées ont compris une combinaison de piéges "pitfall" et d'échantillonnages de la litière du sol le long d'un transect de 250 m de long. Les pièges "pitfall" et les échantillons de la litière du sol ont permis la collecte et l'identification de 24.586 fourmis appartenant à 180 espèces et 25 genres provenant de la RS d'Anjanaharibe-Sud. Les collectes aléatoires ont permis la collecte de 35 autres espèces. Dans la péninsule de Masoala, les piéges "pitfall" et les échantillons de la litière du sol ont permis la collecte et l'identification de 52.307 fourmis appartenant à 167 espèces et 25 genres différents. Les collectes aléatoires au niveau de ce site ont permis la collecte de 30 espèces supplé-

[1] Department of Entomology, University of California, Davis, CA 95616-8584 U.S.A. *Current address:* Life Sciences Division, South African Museum, P.O. Box 61, 8000 Cape Town, South Africa.

mentaires. Le total combiné de la RS d'Anjanaharibe-Sud et de la péninsule de Masoala se monte à 325 espèces et 34 genres.

Pour chaque station d'altitude, deux modes d'estimation, "incidence-based coverage estimator (ICE)" et "first-order jackknife", ont donné des résultats comparables. Les courbes d'accumulation spécifique atteignent une asymptote et démontrent par cela l'efficacité de ces techniques d'inventaire. Les espèces collectées et leur abondance relative sont présentées. La richesse spécifique présente un pic à moyenne altitude. Le taux de renouvellement spécifique et les indices de similarité montrent qu'il existe un changement dans la communauté de fourmis entre la forêt de basse altitude, 875 m et la forêt d'altitude à partir de 1200 m. Le pic de richesse spécifique constaté à moyenne altitude est considéré comme étant le résultat de la conjugaison de la richesse des forêts des communautés rencontrées à basse altitude et en altitude.

Introduction

Although invertebrates and plants make up the vast majority of species in forest habitats, landscape-level patterns of invertebrate biodiversity are little known for tropical ecosystems (Gaston et al., 1993). Such distributional data will largely determine how effective conservation areas are at representing distinct assemblages of species. Species richness, the number of species in a given area, is the currency of biodiversity, but for most groups, we lack knowledge of how to inventory species (Palmer, 1995).

Effective inventory methods must be rapid and repeatable and must contain sufficient subsamples for statistical analysis of species richness and abundance or coverage. Major impediments to developing survey methods and interpreting their results include (1) the effects of scale on species distributions and species turnover; (2) sampling biases due to particular survey methods, habitat differences among sites, and seasonality; (3) problems with completeness of sampling for hyperdiverse groups such as insects; and (4) logistical constraints.

I attempted to address these needs by developing and testing effective sampling and estimation procedures for a hyperdiverse group of terrestrial insects, ants, along elevational gradients in the Réserve Spéciale (RS) d'Anjanaharibe-Sud and on the western Masoala Peninsula, Madagascar. Similar methods were used to inventory ants in the Réserve Naturelle Intégrale (RNI) d'Andringitra (Fisher, 1996a). Specifically, this study tested methods to survey leaf litter ants and evaluated the effect of elevation on species richness. In addition, I compared measures of faunal similarity and species turnover (beta diversity) for

ant species across elevations sampled from 25 m to 1985 m.

Methods

Study Sites

In addition to the survey sites in the RS d'Anjanaharibe-Sud (Chapter 1), surveys were conducted between 13 November and 11 December 1993 on the western side of the Masoala Peninsula in the province of Toamasina. The Masoala Peninsula collection sites were located (1) 6.3 km south of Ambanizana, Andranobe Field Station, 15°41'S, 49°57'E, 1–100 m; (2) 5.3 km south-southeast of Ambanizana, Andranobe Field Station, 15°40'S, 49°58'E, 350–500 m; (3) 6.2 km south-southeast of Ambanizana, Andranobe Field Station, Be Dinta Camp, 15°40'S, 50°00'E, 600 m; and (4) 6.9 km northeast of Ambanizana, Ambohitsitondroina Mountain, 15°34'S, 50°00'E, 800–1080 m. The Ambohitsitondroina Mountains reach a height of 1080 m and are part of the same ridge formation that includes the Andranobe Field Station, which rises to an elevation of 600 m at Be Dinta Camp.

Survey Methods

In the RS d'Anjanaharibe-Sud, intensive ant surveys were conducted at four sites located at 875, 1200, 1565, and 1985 m. An additional partial survey was conducted at 1280 m. On the Masoala Peninsula, intensive surveys were conducted at three sites located at 25, 425, and 825 m. At each elevation the survey method used 50 pitfalls

and 50 leaf litter samples, in parallel lines 10 m apart, along a 250 m transect. The site for each transect was chosen with the intent of sampling representative microhabitats found at each elevation (Palmer, 1995). Pitfall traps were placed and leaf litter samples gathered every 5 m along the transect. Pitfall traps consisted of test tubes (18 mm internal diameter × 150 mm long and partly filled to an approximate depth of 50 mm with soapy water and a 5% ethylene glycol solution), inserted into polyvinyl chloride sleeves and buried with the rim flush with the soil surface. Traps were left in place for 4 days.

I extracted invertebrates from samples of leaf litter (leaf mold and rotten wood) using a modified form of the Winkler extractor (Fig. 4-1) (Besuchet et al., 1987; Fisher, 1996a). The leaf litter samples involved establishing 50 1-m² plots separated by 5 m along the transect line. The leaf litter inside each 1-m² plot was collected and sifted through a wire sieve of 1 cm grid size. Before sifting, the leaf litter material was minced using a machete to disturb ant nests in small twigs and decayed logs. Approximately 2 liters of sifted litter were taken from each 1 m² plot. At low elevations (<800 m), where litter may be sparse, less than 2 liters was sometimes taken. In montane areas, where the litter is often thick, 2 liters was the maximum amount taken at each subsample site. The sifted litter samples were taken back to a tarp-covered laboratory constructed at each camp, and ants were extracted from the sifted litter during a 48-hour period in modified Winkler sacks (Fig. 4-1, "mini-Winkler"). The standard Winkler sack holds up to four 2-liter samples of sifted litter, whereas mini-Winklers are designed to hold only one 2-liter sample. Each sifted litter sample was held in a 0.4 mm grid size mesh sack that was vertically suspended in a larger cotton enclosure. Ants and other invertebrates that worked their way out of drying litter contained in the mesh sack fell through the cloth enclosure into a 0.53-liter plastic bag (Whirl-Pak, Nasco, Fort Atkinson, Wisc.) containing 70% ethanol at the bottom of the mini-Winkler. Because insects are less effectively extracted from wet leaf litter, sifting was done at least 24 h after significant rainfall.

I also surveyed ants through general collecting, defined as any collection that was separate from the mini-Winkler or pitfall transects, including searching in rotten logs and stumps, in dead and live branches, in bamboo, on low vegetation, under canopy moss and epiphytes, under stones, and leaf litter sifting. At each transect site, general collections were conducted for approximately a 2-day period. General collections were made within 1 km and within 75 m in elevation of each transect. These collections included samples of the arboreal ants found on low vegetation that were not sampled by pitfalls or mini-Winklers. Ants sampled with general collection methods, therefore, were not used in the analysis of the efficacy of the survey of the leaf litter ants, faunal similarity, or beta diversity.

At 1280 m in the RS d'Anjanaharibe-Sud, a partial transect of 50 pitfalls and only 26 mini-Winklers was completed. This site was located in a ravine and was characterized by a thick clay soil with a high moisture content. A partial survey was conducted at 1280 m to compare with the 1200 m site, which contained habitats more typical of the elevational zone.

Identification

Specimens were identified to morphospecies level on the basis of characters previously established to be important at the species level for each genus. When possible, species names were attached to these morphospecies by using taxonomic descriptions (see Fisher, 1997, for a list of references) and by comparing specimens with those previously collected by Ward and Fisher in Madagascar that had been compared with type material. Species codes used in this chapter correspond to species codes used in Fisher (1996a). A representative set of specimens will be deposited at the Museum of Comparative Zoology, Harvard University, and in Madagascar.

Data Analysis

Evaluation of Sampling Method—To assess the completeness of the survey for the elevations sampled, I plotted cumulative species per sample curves for each elevation. Species accumulation was plotted as a function of the number of leaf litter and pitfall trap samples taken. For the analysis each leaf litter sample was paired with the adjacent pitfall sample, collectively termed a station sample. For 1280 m in the RS d'Anjanaharibe-Sud, only the first 26 pitfalls were combined with the 26 litter samples. Species accumulation curves for the 50 (26 for 1280 m) stations per transect, as well as incidence-based coverage estimator (ICE) and first-order jackknife estimates of the to-

(a) Litter sifter

- 30 cm diameter metal hoop with handle
- 30 cm diameter metal hoop with handle and 1x1 cm wire mesh.
- heavy cotton cover
- tie
- 13 cm diameter metal ring

30 cm
33 cm
61 cm
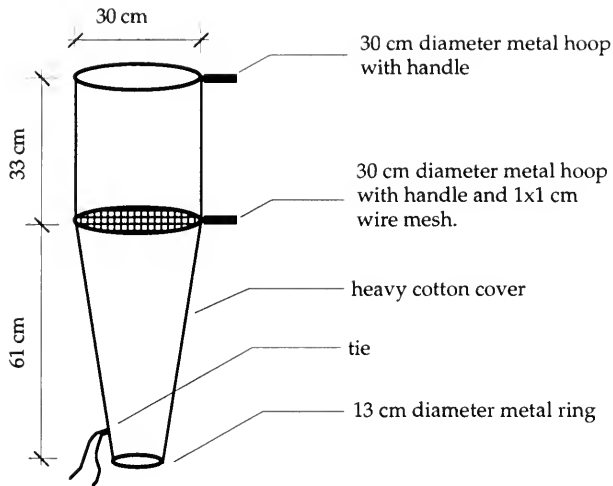
(b) Front view with fabric cover
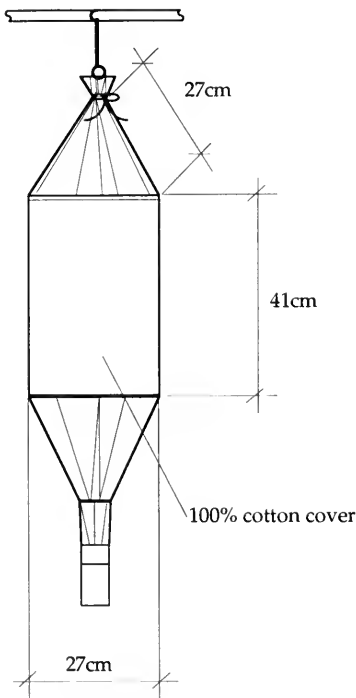
27cm
41cm
27cm
100% cotton cover

(c) 3-Dimensional view without fabric cover

- 3 cm diameter metal ring
- string
- 16x27 cm metal wire support
- 27x36 cm mesh bag, 0.4 mm grid size, to hold leaf litter
- 16x27 cm metal wire support
- 7.5 cm diameter metal ring to funnel cloth
- 6.35 cm diameter metal ring
- plastic cup and plastic bag attached to metal ring

FIG. 4-1.   Litter sifter **(a)** and mini-Winkler sack design. **(b)** Front view with fabric cover and **(c)** three-dimensional view without fabric cover. Litter is first sifted through a 1 cm grid size wire mesh. The sifted litter is placed in the 0.4 mm grid size mesh sack, which is hung vertically in the mini-Winkler enclosure. Ants and other invertebrates leave the litter in the mesh sack and are collected in a plastic bag containing ethanol at the base of the mini-Winkler. The plastic bag is attached to a plastic cup with its bottom removed. At each camp, 25 mini-Winklers are set up under a tarp and hung on wooden poles. Cotton string is looped around the base of each mini-Winkler to stabilize it during windy conditions.

tal number of species in the local community from which the samples were taken, are plotted for each succeeding station sample. The ICE and the first-order jackknife methods are nonparametric approaches to improving the estimate of species richness. The ICE method is based on species found in 10 or fewer sampling units (Lee & Chao, 1994; Chazdon et al., in press). Standard deviations of ICE estimates are based on bootstrap estimates (R. K. Colwell, unpubl.). The first-order jackknife method is based on the observed frequency of unique species (the jackknife estimator and its SD are defined in Heltshe & Forrester, 1983). For species accumulation curves, sample order was randomized 100 times, and the means and SDs of the ICE and jackknife estimates were computed for each succeeding station using the program Estimates (R. K. Colwell, unpubl.; see also Colwell & Coddington, 1994; Chazdon et al., in press). If the species accumulation or jackknife estimate curves approach an asymptote, then the transect length is arguably sufficient. Conversely, if the curves do not begin to flatten out, more intensive sampling may be necessary to accurately compare diversities between elevations. This assumes that for hyperdiverse groups, more intensive sampling (i.e., larger numbers of subsamples) will eventually generate curves that approach, not necessarily reach, an asymptote. With a high number of rare species, these curves may never completely flatten out and reach an asymptote but may continue to slowly increase with more sampling. That is, the entire area may need to be exhaustively surveyed to collect every species.

ANT DIVERSITY—Data on both species richness and abundance were used to assess the change in species composition along the elevational gradient. Only records of ant workers were used in these calculations. Because alates may travel considerable distances during dispersal, their presence does not necessarily signify the establishment of a colony of that species within the transect zone. In addition, collections of queens and males dispersing from nearby nests at the time of the survey may not reflect the relative abundance of the species. Because ants are colonial, abundance measures were based not on the total number of individual workers collected at each transect site but on species frequency (proportion of stations, out of 50, in which each species was collected at a site).

For each elevation, I compared ICE and first-order jackknife estimates of total species richness and 95% confidence limits. Overlap and species turnover (i.e., "complementarity," *sensu* Colwell & Coddington, 1994) of the ant assemblages at different elevations were assessed using faunal similarity and beta diversity indices. Similarity of the ant fauna was assessed using two different measures: (1) the Jaccard Index, which is based on presence and absence data only: $C_J = j/(a + b - j)$, where j = number of species found at both elevations, a = number of species at elevation A, and b = number of species at elevation B (Magurran, 1988); and (2) the simplified Morisita Index, which incorporates abundance data:

$$C_{MH} = \frac{2\Sigma(an_i \times bn_i)}{(da + db)aN \times bN}.$$

where

$$da = \frac{\Sigma an_i^2}{aN^2}$$

and

$$db = \frac{\Sigma bn_i^2}{bN^2}.$$

where aN = total number of station or species occurrences at elevation A, bN = total number of station or species occurrences at elevation B, an_i = the number of stations occupied by the ith species at elevation A, and bn_i = the number of stations occupied by the ith species at elevation B (Horn, 1966; Wolda, 1981). Similarity indices based on presence/absence data, such as the Jaccard, have been shown to be strongly influenced by species richness and sample size (Wolda, 1981). The Morisita Index is nearly independent of species richness and sample size (Wolda, 1981) and therefore may be more appropriate for comparisons of ant assemblages along an elevational gradient.

Beta diversity (species turnover between elevations) was calculated in two ways. First, the beta diversity measure of Whittaker (1960) was used: beta-1 = $(S/a) - 1$, where S = the total number of species in the two elevations combined and a = the mean number of species in each elevation. Because this measure does not distinguish between species turnover and the loss of species along a gradient without adding new species, the measure of beta diversity developed by Harrison et al. (1992) was also calculated: beta-2 = $(S/a_{max}) - 1$, where S = the same as beta-1 above and a_{max} = the maximum value of alpha diversity (i.e., number of species) among the elevations compared.

The number of species unique to an elevation and the number of species shared between elevations were also compared. These comparisons incorporated elevational sites from both localities but excluded the partial transect at 1280 m. The number of species unique to 875 was calculated in the absence of the 825 m site. Likewise, 875 m site data were not used in calculating species unique to the 825 m site.

Results

In the RS d'Anjanaharibe-Sud, I collected and identified 28,248 ants representing 215 species and 30 genera from general collections and the leaf litter and pitfall methods. These included 553 queens and 211 males. The leaf litter and pitfall methods yielded 24,586 worker ants belonging to 180 species. On the Masoala Peninsula, I collected and identified 54,263 ants representing 197 species and 31 genera from general collections and the leaf litter and pitfall methods. These included 474 queens and 22 males. The leaf litter and pitfall methods produced 52,307 ants representing 167 species and 25 genera. For the RS d'Anjanaharibe-Sud and the Masoala Peninsula combined, a total of 325 species and 34 genera were collected from all methods. From the pitfall and leaf litter methods, a total of 271 species were collected, with 76 species shared between localities. Lists of ant species in the RS d'Anjanaharibe-Sud (Table 4-1) and the Masoala Peninsula (Table 4-2), based on all collecting techniques and separated by elevation and technique, are presented. For the Masoala Peninsula, general collections at 600 m and from 950 to 1080 m are also presented (Table 4-2). Absent from Table 4-1 are records of species from the RS d'Anjanaharibe-Sud known from queens only (*Serrastruma ludovici* from 875 m and *Camponotus* sp. 31 from 1985 m).

Within the RS d'Anjanaharibe-Sud, the 875 m zone had the greatest total number of species recorded (125 species total from all methods; 97 species total from litter and pitfall samples; Table 4-1). If the data for 1200 and 1280 m are combined, the number of species is similar to that from 875 m (117 species total from all methods; 100 species total from litter and pitfall samples). On the Masoala Peninsula, the total number of species was greatest at 825 m (112 species total

from all methods; 109 species total from litter and pitfall samples).

The number of species and number of individuals collected from pitfall traps were low compared to those collected by the mini-Winkler method, except for 1280 m in the RS d'Anjanaharibe-Sud, where two pitfall traps collected an exceptional number (a total of 1,183 individuals) of *Paratrechina* sp. 5. Only 10 species were collected by pitfall traps that were not also collected by the mini-Winkler method. Five of the 10 were *Leptogenys* species, which are large, fast-moving terrestrial (epigaeic) species with solitary foragers. In dry forest in southwestern Madagascar, however, pitfall traps collected a greater number of individuals and species (Fisher & Razafimandimby, 1997).

The abundance of ant species is presented in Table 4-3 for the RS d'Anjanaharibe-Sud and in Table 4-4 for the Masoala Peninsula. Both the proportion of stations at which each species was collected and the number of individuals collected are given. General collections are not included. In the RS d'Anjanaharibe-Sud, only one species of 180, *Paratrechina* sp. 5, was found at all elevations. The relative frequency of occurrence of *Paratrechina* sp. 5, however, differed considerably from one site to the next (0.06 and 0.02 at 875 m and 1985 m, respectively, and 0.46, 0.42, and 0.54 at 1200, 1280, and 1565 m, respectively; Table 4-3). Excluding the partial transect at 1280 m, only 10 species were found at three of the four elevational sites. On the Masoala Peninsula, 30 species out of 167 (18%) were found at all three elevations sampled.

The number of ant species and abundance, measured as the total number of stations at which each species was collected, peaked at the mid-elevations and quickly decreased at high elevations (Fig. 4-2). The 825 m (Masoala Peninsula) site was the highest in species richness, and the 425 m site (Masoala Peninsula) had the highest abundance. There is also a significant relationship between the total number of individuals and the total number of stations at which each species was collected at a site (Tables 4-1, 4-2; for all elevations with complete transects, $r^2 = .66$, $p = 0.027$).

The relative prevalence of each subfamily for the combined pitfall and leaf litter samples is shown in Table 4-5. The fauna was dominated by Myrmicinae in both number of species and number of individuals, followed by the Ponerinae. Between localities, the taxonomic ratio of Ponerinae

TABLE 4-1. Ant species list for the RS d'Anjanaharibe-Sud, including elevation and collection method.*

Genus	Species	875 m	1200 m	1280 m	1565 m	1985 m
CERAPACHYINAE						
Cerapachys	1	G	W, G			
	5	W	W			
	7	W, G				
	10	G				
	11	G				
	12	W				
	14	W	W			
	15	W				
	16	W				
	17		W	W		
	18		W	W, P		
	19				P	
	20				W, G	
	21			W		
	22		G			
Simopone	3	G				
	4	G				
	5		G			
DOLICHODERINAE						
Technomyrmex	4		P			
FORMICINAE						
CAMPONOTINI						
Camponotus	5		W, P	W, G		
	6	G				
	16	W, G	W, P, G	W	W	
	17		G		W, G	
	19	P, G	G			
	20		G			
	21	G	W		W	
	23		G		G	
	24	W, G				
	26	G				
	27		G			
	28		W, G		W	
	32		W			
	33		W			
	35	G	W, G			
	37	G		G		
	38		G			
	39					W, P, G
	40	W, G				
	hildebrandti	W, G				
	nasica		G	G		
	putatus	G				
LASIINI						
Paratrechina	1	W, G	W, P, G		W	
	5	W, G	W, P, G	W, P, G	W, P, G	P
	6	W, G	W, G	W	W, G	
	11	W	W			
PLAGIOLEPIDINI						
Plagiolepis	2	G				
MYRMICINAE						
CATAULACINI	3	G	W,G		W	
Cataulacus	1	G				
	oberthueri	G				
	regularis	G				

TABLE 4-1. *Continued.*

Genus	Species	875 m	1200 m	1280 m	1565 m	1985 m
CREMATOGASTRINI						
Crematogaster	3	W, G				
	5	W, P, G	W, P, G		W, G	
	7	W	G			
	10		W, P, G	W	W, G	
DACETONINI						
Kyidris	1	W, G	W			
Smithistruma	4		G			
	5				W, G	
Strumigenys	1		G, W	W		
	13	W	W			
	19	W, G				
	22	W	W			
	24	W	W			
	25		W, P		W	
	26	W				
	31				W	
	32				W	
	33		W	W		
	34	W				
	35	W, P				
	36	W				
	38		W, G			
	39	W	W	W, G	W	
	40			W	W	
	41				W	
	42				W	W
	43			W		
	44				W	
	51	W				
	52	W	W, G			
	54		W	W		
	56			W, G		
MYRMICINI						
Eutetramorium	*mocquerysi*	P, G				
PHEIDOLINI						
Pheidole	8	P	W, P	W		
	13	G	W, G			
	23				W	
	30				W, P, G	W, P, G
	36				W, P, G	
	37	W	W, P	W, P	W, P, G	
	38		G	W, P	W, P, G	
	39				G	
	40				W	
	41	W, G	W, P, G	W, P		
	42	W, G	W, P, G			
	43	W, P, G				
	44	W, G	W, P	W		
	45			W, P		
	46			W		
	47		W, P	W, P, G		
	48		W, P			
	49		W, P, G			
	50	W	W			
	51	W	W, P			
	52		W, G			
	53	W, P				

TABLE 4-1. *Continued.*

Genus	Species	875 m	1200 m	1280 m	1565 m	1985 m
	54	W, P				
	55	W, G				
	56	W, G				
	57	W, P				
	58	W, P				
	68		W			
	71	W				
	veteratrix	W, P, G	W, P	W, P		
PHEIDOLOGETONINI						
Oligomyrmex	3	W, G	W			
	6	W	W	W, P		
PODOMYRMIINI						
Terataner	1	G				
SOLENOPSIDINI						
Monomorium	1		W	W	W	
	4				W, G	
	7		W			
	14	W				
	16	W	W			
	20					W, G
	26	W				
	27				W, G	W
	31		W			
	35	W				
	37	W, G				
	38	W	W	W		
	39	W	W	W	W	
	40		W			
TETRAMORIINI						
Tetramorium	6	W, G	W, G			
	14		W, P, G	W, P	W, P, G	
	19	G				
	23	W, P, G	W			
	25	G	W			
	28				G	
	29	G	W, G	W, G		
	37	W, P	W, P	W, P	W	
	38	G	G		G	
	39		G			
	40	W, P, G	W	W, G	W	
	44					W
	45			W		
	46		W			
	47			W		
	48			W		
	49		W			
	50	W, P, G		W	W, P	
	51	W				
	52				P	
	andrei	W, P, G	W, G		W, P, G	
	dysalum	W				
	naganum	W, P	W, P	W, P, G		
	schaufusii		W, G	W	W	
	tosii	W, G				
INCERTAE SEDIS						
Undescribed genus	4		W, P	W	W, G	
	5				W, P, G	W, P, G

TABLE 4-1. *Continued.*

Genus	Species	875 m	1200 m	1280 m	1565 m	1985 m
PONERINAE						
AMBLYOPONINI						
Amblyopone	5	W		W		
Mystrium	1	W				
	3	P				
	5	W				
Prionopelta	1	W, G	W			
	3	W, G				
	4	W	W	W		
	6		G			
ECTATOMMINI						
Discothyrea	1		W	W	W	
	4	W	W			
	5	W				
Proceratium	4	W				
	5	W				
	6		W	W	W	
PONERINI						
Anochetus	*grandidieri*	W	W			
Hypoponera	1		W	W	W	
	6			W		
	9	W				
	11		W, G	W	W	
	19				W, G	
	20					W, P
	21		W	W	W	
	22				W, G	
	23		W		W	
	24				W, G	
	25		W, G	W, G		
	26		W	W		
	28		W	W		
	29		W			
	30		W			
	31	W				
	32	W				
	34	W				
	35	W				
	36	W				
	37	W				
	38	W				
	39	W				
	40	W				
	41	W, G				
	42	W				
	47	W				
	sakalava	W, G	W, G	W, G	G	
Leptogenys	5	P				
	9	W, G				
	10	G				
	11	G			P	
	14			P		
Odontomachus	*coquereli*	W, G				
Pachycondyla	1	W, G	W			
	3		W			
	cambouei	W, P, G	W	W, P		
	perroti	G				
	sikorae		G			

TABLE 4-1. *Continued.*

Genus	Species	875 m	1200 m	1280 m	1565 m	1985 m
PSEUDOMYRMECINAE						
Tetraponera	cf. *grandidieri*	G				
	psw-*70*	G				
	psw-*92*	G	G			
Total species: G		65	43	12	25	4
Total species: P		20	22	14	12	5
Total species: W		92	85	52	47	8
Total species: W and P		**97**	**86**	**53**	**50**	**9**
Total species: All methods		**125**	**103**	**55**	**55**	**9**
Number (%) of unique species: All methods		70 (56%)	25 (24%)	10 (18%)	17 (31%)	4 (44%)
Number (%) of unique species: W and P		55 (57%)	20 (23%)	9 (17%)	17 (34%)	4 (44%)
Total number of G collections		85	55	11	36	18
Number of workers: G		1,151	663	87	733	264
Number of workers: P		175	440	1,741	293	48
Number of workers: W		6,661	6,033	1,393	6,130	1,672
Total number of workers		**7,960**	**7,136**	**3,221**	**7,156**	**1,984**
Abundance		941	759	256	442	151

* Only collections of workers are presented (G = general collections; P = pitfall transect samples; W = mini-Winkler leaf litter transect samples). A total of 213 ant species and 27,484 workers were collected. In addition, *Serrastruma ludovici* (875 m) and *Camponotus* sp. 31 (1985 m) were recorded from queens only. Abundance refers to the total number of stations at which each species was collected.

to Myrmicinae was similar: 0.51 in the RS d'Anjanaharibe-Sud and 0.45 on the Masoala Peninsula. The taxonomic ratio, however, differed between elevations, peaking at midelevation (Table 4-5).

Observed number of species, ICE and first-order jackknife estimates of species richness, their SDs, and their 95% confidence intervals are presented for the RS d'Anjanaharibe-Sud and the Masoala Peninsula (Table 4-6). Species accumulation curves for observed number of species and ICE and jackknife estimates approached an asymptote but were still increasing slowly (Fig. 4-3, the RS d'Anjanaharibe-Sud; Fig. 4-4, the Masoala Peninsula). This indicates that within the area of the survey, the technique used collected the majority of ants foraging and living in the leaf litter in the area encompassed by the 250 m transect and that with increased sampling effort using the same methods (i.e., adding more pitfall and litter stations) in the same area, only marginal increases in species richness should be attained. In a combined analysis of the elevations in the RS d'Anjanaharibe-Sud (Fig. 4-3f) and on the western Masoala Peninsula (Fig. 4-4d), the pitfall and mini-Winkler methods collected 84% and 86%, respectively, of the total number of leaf litter ant species estimated by the first-order jackknife method to occur in each region.

Faunal similarity values based on presence/absence data (Jaccard Index) and abundance (simplified Morisita Index) are presented for the RS d'Anjanaharibe-Sud and the Masoala Peninsula (Table 4-7). The Morisita Index, which relies on abundance data, is less affected by strong differences in species richness between elevations than the Jaccard Index. In the RS d'Anjanaharibe-Sud, Jaccard similarity values were lowest between 1985 m, which contained only nine species, and the three other elevations (875, 1200, and 1565 m). The lowest Morisita values were between 875 and 1565 m, between 875 and 1985 m, and between 1200 and 1985 m. Jaccard values were similar between the 875 and 1200 m sites (0.230) and the 1200 and 1565 m sites (0.236). The Morisita similarity value for the 875–1200 m sites (0.272) was greater than that for the 1200–1565 m sites (0.198). On the Masoala Peninsula, the lowest similarity was between 25 and 825 m. The lowest similarity between adjacent elevations was between 425 and 825 m. The 875 m site in the RS d'Anjanaharibe-Sud was more similar to the 825 m site on the Masoala Peninsula than it was to the 1200 m in the RS d'Anjanaharibe-Sud. Likewise, the 825 m site was more similar to the 875 m site than it was to the 425 m site on the Masoala Peninsula (Table 4-7). The overall Jaccard Index value of similarity between all elevations in the two localities was 0.278.

Beta diversity values showed related trends in

TABLE 4-2. Ant species list for the western Masoala Peninsula, including elevation and collection method.*

Genus	Species	25 m	425 m	600 m	825 m	950–1080 m
CERAPACHYINAE						
Cerapachys	1			G	W, G	G
	5				W	
	7		W		W, G	
	13				W	
	14				W, G	
	16				W	
	22	W, G	W, G		W	
DOLICHODERINAE						
Tapinoma	1	G				
Technomyrmex	1			G		
	3		W		W	
	albipes	G				
FORMICINAE						
CAMPONOTINI						
Camponotus	2				W, G	
	5	G	W, G		W, G	
	12				W, G	
	15				W	
	16	W, G	W	G	W, P	
	18			G		G
	19			G		G
	22					G
	24		W, G	G	W, G	G
	25	G				
	28		W, G			G
	29					G
	30		W, P, G		W, P	
	32					G
	34	G	G			G
	35	W, G	W	G	W	G
	36			G		
	mocquerysi	G				
	putatus		W			
LASIINI						
Paratrechina	1	W, P				
	5	W, P	W, P		W, P, G	
	6	W	W, G		W, G	G
	8		W, P	G	W, P, G	G
	9	G	W			
	10	W, P				
PLAGIOLEPIDINI						
Plagiolepis	3	W	W		W	G
MYRMICINAE						
CATAULACINI						
Cataulacus	1	G		G		
	oberthueri			G		
CREMATOGASTRINI						
Crematogaster	3	W	W		W	
	7				G	
	8	W	W			
	9	W, G	W, G			
	12				W	
	schenki				W	

TABLE 4-2. *Continued.*

Genus	Species	25 m	425 m	600 m	825 m	950–1080 m
DACETONINI						
Kyidris	1	W	W, G		W, G	
Smithistruma	6	W	W		W	
	7	W	W, G			
Strumigenys	1		W		W	
	13	W	W		W	
	14	W	W, G		W	
	19		W		W	
	22	W	W		W	
	23				W	
	24	W	W			
	25	W	W		W	
	26	W	W		W	
	27	W	W, G			
	28	W	W		W	
	29		W		W	
	30				W	
	37		W			
	51				W, G	
	52				W	
	53	W	W, G			
	55				W	
FORMICOXENINI						
Leptothorax	3					G
PHEIDOLINI						
Aphaenogaster	gonacantha		W, P, G	G		
Pheidole	8					G
	13				W	
	20	W, P	W, P			
	23	W				
	41				W	
	43	W, P, G	W, P			
	44	W, P	W, P		W, P	
	49				W, P	
	50	W	W, P		W	
	52				W	
	53	W, P, G	W		W, P	
	54				W	
	55				G	
	58	G	W		W, P	
	60	G				
	61			G		
	62				W	
	63				W, P, G	
	64				W	
	65				W	
	66				W	
	67				W	
	68	W, P	W, P, G			
	69	W, P	W, P			
	70	W, P	W			
	71	W, P	W			
	72		W, G			
	73	W, P	W, P			
	74	W				
	oswaldi	W, P, G	W, P, G			
	spinosa	W, P, G	W, P			
	veteratrix				W, P, G	G

TABLE 4-2. *Continued.*

Genus	Species	25 m	425 m	600 m	825 m	950–1080 m
PHEIDOLOGETONINI						
Oligomyrmex	3	W, P, G			W	
	6	W	W, P		W	
PODOMYRMINI						
Terataner	*alluaudi*	G				
SOLENOPSIDINI						
Monomorium	2				W	
	5		W		W	
	7		W		W, G	
	14	W, P	W			
	23		W, P, G		W, P, G	
	24				W, P, G	
	26	W	W			
	28				W	
	32					G
	33				W	
	34				W, P, G	
	36	W	W		W	
	38				W	
	39	W	W		W	
	41		W	G		
	42	W			W	
TETRAMORIINI						
Tetramorium	6	G	W		W, G	
	7	W			W	
	16	W	W, P, G			
	21	W, G†	W, P, G			
	23	W, P, G	W, P		G	
	24				W, P, G	
	25		P, G		W	
	26		P			
	29				W	G
	34	W	W, P			
	35	W				
	36		W, P, G			
	37		W, G		W, P, G	
	39				W	
	40	W	W, G		W, G	
	41	W	W, P, G			
	42		W			
	43	W	W			
	andrei	W, P, G	W, P		P	
	bicarinatum	G				
	dysalum	W, P, G	P, G		W	
	electrum				W	
	marginatum		W, P, G		W	
	naganum	W, P	W		W, P, G	
	tosii	W, G	W, P, G			
INCERTAE SEDIS						
Undescribed genus	2				W, G	
	3	W	W, G			
PONERINAE						
AMBLYOPONINI						
Amblyopone	1		W			
	4				W	
Mystrium	3				W	
	4	W, P, G	W, P, G			
	5		W			

TABLE 4-2. *Continued.*

Genus	Species	25 m	425 m	600 m	825 m	950–1080 m
Prionopelta	1	W	W, P, G		W, G	
	4				W, G	G
	5	W	W, G			
ECTATOMMINI						
Discothyrea	3				W, G	
	5		W		W, G	
	6	W				
	7		W			
Proceratium	2	W, P, G	W			
	diplopyx				W	
PLATYTHYREINI						
Platythyrea	*bicuspis*			G		
PONERINI						
Anochetus	*grandidieri*	W, P	W, G		W, G	
Hypoponeura	22				W	
	26		W		W, G	
	29				W	
	32	W, P	W			
	33	W, P	W			
	36	W, P, G	W, P			
	38				W	
	39				W	
	43	W, G	W, P			
	44	W	W			
	45	G				
	46	W	W		W	G
	47		W		W	
	48				W	
	49				W	
	50				W, G	
	51		W			
	52	W				
	sakalava	W, G	W	G	W, G	
Leptogenys	4		W			
	5				W	
	6				P	
	7				P	
	8	G[+]				
	11				W	
Odontomachus	*coquereli*		W, G		W, G	G
Pachycondyla	1				W	
	2	W, P	W, P, G			
	cambouei	W, P	W, P, G		W, P	
	perroti	W, P, G		G		
Ponera	1	W	W, G			
PSEUDOMYRMECINAE						
Tetraponera	*grandidieri*	G		G		G
	longula	G				
Total species: G		37	37	18	36	22
Total species: P		29	33	20		
Total species: W		76	98		106	
Total species: W and P		**76**	**101**		**109**	
Total species: All methods		**93**	**102**		**112**	
Number (%) unique species: All methods		17 (18%)	11 (11%)	5 (28%)	53 (47%)	6 (27%)
Number (%) of unique species: W and P		8 (11%)	15 (15%)		55 (50%)	
Total number of G collections		48	22	22	25	33
Number of workers: G		367	325	150	403	215
Number of workers: P		884	569		1,661	
Number of workers: W		14,980	21,827		12,386	

TABLE 4-2. *Continued.*

Genus	Species	25 m	425 m	600 m	825 m	950–1080 m
Total number of workers		**16,231**	**22,721**		**14,450**	
Abundance		905	1,087		1,007	

* Only collections of workers are presented (G = general collections; P = pitfall transect samples; W = mini-Winkler leaf litter transect samples). A total of 213 ant species and 27,484 workers were collected. Abundance refers to the total number of stations at which each species was collected.

† Samples from 150 m.

levels of species turnover between adjacent elevations with greatest species turnover at midelevations (Table 4-8). In the RS d'Anjanaharibe-Sud, the 1985 m site had a high beta-1 value in comparison to other elevations because of the few numbers of species present (compare to beta-2). Because of the loss of species with elevation, beta-2 is the preferred measure of species turnover. Excluding 1280 m, the highest beta-2 value was between the 875 and 1200 m sites. On the Masoala Peninsula, the highest value of beta-2 was between 425 and 825 m. In comparison between the two localities, species turnover was similar along the elevational gradient. In the RS d'Anjanaharibe-Sud, the 875–1565 m beta-2 value was 0.392, and on the Masoala Peninsula, the 25–825 m beta-2 value was a similar 0.394. The overall beta-2 values of species turnover between all elevations at both localities were also similar, 0.568 and 0.511, respectively (Table 4-8).

The 825 and 875 m sites had the greatest number of species unique to an elevation (Table 4-9). The 1985 m site, however, had the highest percentage of species unique to an elevation (Table 4-9). The midelevation sites shared the highest number of species with other sites when compared to the 25 m and higher elevation ($\geq$1200 m) sites. The 25 and 425 m sites had many species in common, but the 425, 825, and 875 m sites shared more species with higher elevations.

Discussion

Elevational Gradient and Complementarity

Species richness did not decrease monotonically as a function of elevation. When the data from the RS d'Anjanaharibe-Sud and the Masoala Peninsula are combined, there is a peak in richness at 800–900 m (Fig. 4-2). A midelevation peak has been documented for a few taxa in the tropics (see

review in Rahbek, 1995), including ants in Panama (Olson, 1994). The generally accepted pattern, however, is that species richness declines with elevation (Rahbek, 1995), and this pattern is analogous to the latitudinal gradient (Stevens, 1992). The midelevation peak observed in ant species richness in Madagascar may be the result of a mixing of two distinct ant assemblages along an ecotone (see below).

After the midelevation peak, species richness declines rapidly, reaching a minimum of nine species at 1985 m (Fig. 4-2). Species richness was also found to decrease rapidly with increasing elevation above 800 m in the RNI d'Andringitra (Fisher, 1996a) and in Panama (Olson, 1994). This rapid decrease in species richness probably reflects climatic variables, mainly the reduction of radiant energy, which may affect larval development and worker foraging activities (Brown, 1973; Fisher, 1996a) and decrease primary productivity (Rosenzweig & Abramsky, 1993).

Faunal similarity and beta diversity measures (Tables 4-7 and 4-8) suggest a division of the ant fauna into two communities, one occurring in lowland forests at $\leq$875 m and the other in montane forests at $\geq$1200 m. Species turnover was greatest at midelevation. The same pattern was found in the RNI d'Andringitra (Fisher, 1996a), where the greatest turnover in ant species assemblages occurred between transects conducted at midelevation (785 and 825 m) and the 1275 m zone.

Analysis of the midelevation taxa is complicated by the separation of the lower elevation sites on the Masoala Peninsula from the higher sites in the RS d'Anjanaharibe-Sud. The high number of species unique to 825 and 875 m (Table 4-9) is a biased result. Both the 825 and 875 m sites were compared to higher and lower sites, respectively, in the other locality. For example, the 875 m site in the RS d'Anjanaharibe-Sud was compared with the 425 m site from the Masoala Peninsula. A certain proportion of the species unique to the 825

Genus	Species	875 m	1200 m	1280 m	1565 m	1985 m
CERAPACHYINAE						
Cerapachys	**1**		0.06 (25)			
	5	0.10 (26)	0.02 (1)			
	7	0.02 (5)				
	12	0.04 (3)				
	14	0.02 (3)	0.04 (3)			
	15	0.02 (1)				
	16	0.04 (7)				
	17		0.06 (9)	0.02 (1)		
	18		0.06 (11)	0.02 (1)		
	19				0.02 (1)	
	20				0.10 (15)	
	21			0.04 (2)		
DOLICHODERINAE						
Technomyrmex	4		0.02 (1)			
FORMICINAE						
CAMPONOTINI						
Camponotus	**5**		0.06 (5)	0.02 (1)		
	16	0.04 (2)	0.14 (23)	0.02 (5)	0.04 (2)	
	17				0.04 (19)	
	19	0.02 (1)				
	21		0.04 (11)		0.02 (1)	
	24	0.02 (1)				
	28		0.06 (11)		0.02 (6)	
	32		0.14 (33)			
	33		0.02 (1)			
	35		0.02 (3)			
	39					0.22 (56)
	40	0.04 (19)				
	hildebrandti	0.02 (2)				
LASIINI						
Paratrechina	**1**	0.78 (673)	0.22 (44)		0.04 (21)	
	5	0.06 (50)	0.46 (1,765)	0.42 (527)	0.54 (3,972)	0.02 (1)
	6	0.50 (350)	0.06 (46)	0.04 (10)	0.08 (11)	
	11	0.04 (2)	0.06 (9)			
PLAGIOLEPIDINI						
Plagiolepis	**3**		0.80 (127)		0.02 (1)	
MYRMICINAE						
CREMATOGASTRINI						
Crematogaster	**3**	0.06 (15)				
	5	0.34 (22)	0.10 (5)		0.02 (2)	
	7	0.02 (1)				
	10		0.08 (4)	0.02 (1)	0.06 (3)	
DACETONINI						
Kyidris	**1**	0.32 (233)	0.10 (66)			
Smithistruma	5				0.16 (12)	
Strumigenys	**1**		0.54 (210)	0.14 (24)		
	13	0.04 (3)	0.02 (2)			
	19	0.04 (2)				
	22	0.34 (30)	0.08 (4)			
	24	0.54 (151)	0.02 (1)			
	25		0.34 (64)		0.02 (1)	
	26	0.42 (107)				
	31				0.04 (6)	
	32				0.02 (1)	

TABLE 4-3. *Continued.*

Genus	Species	875 m	1200 m	1280 m	1565 m	1985 m
	33		0.02 (1)	0.02 (1)		
	34	0.64 (154)				
	35	0.46 (119)				
	36	0.04 (2)				
	38		0.06 (3)			
	39	0.02 (2)	0.34 (28)	0.20 (16)	0.40 (39)	
	40			0.02 (3)	0.30 (22)	
	41				0.08 (7)	
	42				0.02 (1)	0.22 (21)
	43			0.02 (1)		
	44				0.02 (1)	
	51	0.02 (1)				
	52	0.04 (2)	0.24 (32)			
	54		0.18 (13)	0.02 (1)		
	56			0.06 (4)		
MYRMICINI						
Eutetramorium	*mocquerysi*	0.02 (1)				
PHEIDOLINI						
Pheidole	8	0.06 (8)	0.18 (25)	0.06 (31)		
	13		0.02 (1)			
	23				0.02 (1)	
	30				0.62 (374)	0.96 (1,166)
	36				0.46 (176)	
	37	0.06 (8)	0.08 (11)	0.20 (44)	0.66 (190)	
	38			0.02 (1)	0.34 (264)	
	40				0.02 (1)	
	41	0.02 (1)	0.86 (484)	0.08 (26)		
	42	0.02 (1)	0.20 (21)			
	43	0.44 (69)				
	44	0.52 (454)	0.06 (13)	0.02 (21)		
	45			0.26 (160)		
	46			0.06 (9)		
	47		0.08 (13)	0.08 (19)		
	48		0.64 (530)			
	49		0.26 (57)			
	50	0.40 (166)	0.06 (10)			
	51	0.02 (2)	0.14 (23)			
	52		0.04 (2)			
	53	0.24 (103)				
	54	0.06 (12)				
	55	0.02 (1)				
	56	0.26 (69)				
	57	0.16 (37)				
	58	0.08 (8)				
	68		0.02 (1)			
	71	0.02 (1)				
	veteratrix	0.84 (335)	0.20 (109)	0.06 (25)		
PHEIDOLOGETONINI						
Oligomyrmex	**3**	0.56 (303)	0.54 (163)			
	6	0.46 (203)	0.26 (49)	0.18 (21)		
SOLENOPSIDINI						
Monomorium	1		0.04 (5)	0.04 (2)	0.24 (54)	
	4				0.20 (137)	
	7		0.06 (6)			
	14	0.06 (6)				
	16	0.04 (2)	0.24 (59)			
	20					0.10 (7)
	26	0.02 (1)				

TABLE 4-3. *Continued.*

Genus	Species	875 m	1200 m	1280 m	1565 m	1985 m
	27				0.16 (95)	0.02 (1)
	31		0.02 (4)			
	35	0.26 (69)				
	37	0.08 (41)				
	38	0.44 (88)	0.38 (86)	0.14 (12)		
	39	0.48 (308)	0.64 (666)	0.32 (166)	0.08 (22)	
	40		0.02 (2)			
TETRAMORIINI						
Tetramorium	**6**	0.26 (39)	0.20 (14)			
	14		0.60 (332)	0.04 (6)	0.42 (55)	
	23	0.44 (44)	0.10 (6)			
	25		0.08 (11)			
	29		0.08 (6)	0.04 (13)		
	37	0.04 (3)	0.26 (55)	0.12 (12)	0.06 (3)	
	40	0.84 (379)	0.22 (36)	0.12 (22)	0.08 (4)	
	44					0.04 (27)
	45			0.08 (4)		
	46		0.02 (1)			
	47			0.02 (1)		
	48			0.08 (12)		
	49		0.06 (14)			
	50	0.54 (88)		0.02 (5)	0.30 (24)	
	51	0.04 (15)				
	52				0.02 (1)	
	andrei	0.64 (226)	0.18 (71)		0.20 (163)	
	dysalum	0.02 (1)				
	naganum	0.12 (11)	0.20 (59)	0.46 (97)		
	schaufusii		0.12 (14)	0.06 (3)	0.24 (17)	
	tosii	0.14 (18)				
INCERTAE SEDIS						
Undescribed genus	4		0.06 (12)	0.06 (5)	0.38 (39)	
	5				0.32 (64)	0.68 (166)
PONERINAE						
AMBLYOPONINI						
Amblyopone	5	0.02 (3)		0.06 (3)		
Mystrium	1	0.20 (23)				
	3	0.02 (1)				
	5	0.04 (2)				
Prionopelta	**1**	0.42 (73)	0.12 (9)			
	3	0.80 (717)				
	4	0.06 (11)	0.24 (29)	0.10 (5)		
ECTATOMMINI						
Discothyrea	1		0.04 (3)	0.04 (2)	0.02 (1)	
	4	0.04 (3)	0.04 (2)			
	5	0.04 (2)				
Proceratium	4	0.04 (8)				
	5	0.04 (3)				
	6		0.02 (1)	0.02 (1)	0.06 (3)	
PONERINI						
Anochetus	*grandidieri*	0.08 (12)	0.02 (1)			
Hypoponera	1		0.14 (18)	0.14 (37)	0.08 (10)	
	6			0.08 (24)		
	9	0.02 (7)				
	11		0.04 (4)	0.06 (3)	0.92 (385)	
	19				0.06 (3)	
	20					0.76 (275)
	21		0.06 (6)	0.14 (15)	0.24 (23)	

TABLE 4-3. *Continued.*

Genus	Species	875 m	1200 m	1280 m	1565 m	1985 m
	22				0.46 (163)	
	23		0.22 (13)		0.04 (2)	
	24				0.06 (4)	
	25		0.90 (397)	0.24 (25)		
	26		0.66 (175)	0.30 (89)		
	28		0.72 (257)	0.06 (17)		
	29		0.04 (4)			
	30		0.06 (8)			
	31	0.04 (4)				
	32	0.52 (159)				
	34	0.22 (15)				
	35	0.04 (2)				
	36	0.50 (149)				
	37	0.04 (8)				
	38	0.78 (289)				
	39	0.18 (24)				
	40	0.02 (1)				
	41	0.08 (115)				
	42	0.02 (7)				
	47	0.02 (1)				
	sakalava	0.10 (11)	0.02 (2)	0.04 (7)		
Leptogenys	**5**	0.02 (7)				
	9	0.02 (1)				
	11				0.02 (1)	
	14			0.02 (1)		
Odontomachus	*coquereli*	0.04 (2)				
Pachycondyla	**1**	0.02 (3)	0.02 (1)			
	3		0.04 (2)			
	cambouei	0.52 (63)	0.10 (7)	0.14 (7)		

* The number of individual workers collected is given in parentheses. Species listed in boldface type were also collected on the Masoala Peninsula (Table 4-4).

and 875 m sites is probably due to differences in the faunal composition between the RS d'Anjanaharibe-Sud and the Masoala Peninsula localities. Therefore, fewer unique species would have been expected from the 825 and 875 m sites if a higher or lower elevation site could have been sampled from the same locality.

Why does species richness increase above 25 m before declining to nine species at 1985 m? Results on the number of shared species between elevations and on species turnover, which suggests a lowland and montane ant fauna, may help explain this pattern. Adjacent elevations share taxa because they may contain similar habitats and because the width of the elevational zones along the gradient is narrow. The proximity of elevational zones encourages the establishment of marginal populations from adjacent elevations (Pulliam, 1988; Stevens, 1989; Rahbek, 1997). Therefore, adjacent elevation sites share species because they are close in space.

Species richness may be highest at midelevations because they are adjacent to the source pool of the distinct montane ant fauna as well as those from lower elevations. A mixing of the lowland and montane ant assemblages results in the peak in species richness. The midelevation sites share the highest number of species with other sites when compared to the lowest and highest elevations (Table 4-9). The number of species shared with the 25 m site decreases rapidly with elevation. The low-elevation sites are bounded and can only receive species spillover from above, mostly from the adjacent midelevations, with which they already share a high proportion of species.

The effects of abundance on observed species richness could explain differences in observed species richness among elevations (Chazdon et al., in press). Species richness at a site may be a function of abundance: the greater the abundance at an elevation, the higher the species richness. In this study, the relationship between abundance, measured as the total number of stations at which each species was collected, and elevation mirrored that of species richness, but abundance peaked at a lower elevation (Fig. 4-2). There is

TABLE 4-4. Abundance, measured as frequency of occurrence (proportion of stations out of 50 paired pitfall and leaf litter samples at which each species was recorded) for each elevation on the Masoala Peninsula.*

Genus	Species	25 m	425 m	825 m
CERAPACHYINAE				
Cerapachys	**1**			0.08 (19)
	5			0.60 (17)
	7		0.02 (1)	0.12 (18)
	13			0.02 (1)
	14			0.06 (23)
	16			0.02 (15)
	22	0.04 (2)	0.08 (16)	0.06 (20)
DOLICHODERINAE				
Technomyrmex	3		0.08 (361)	0.04 (3)
FORMICINAE				
CAMPONOTINI				
Camponotus	2			0.02 (1)
	5		0.02 (7)	0.04 (5)
	12			0.02 (10)
	15			0.02 (2)
	16	0.02 (2)	0.14 (17)	0.04 (3)
	24		0.08 (19)	0.02 (1)
	28		0.02 (1)	
	30		0.04 (4)	0.08 (11)
	35	0.06 (3)	0.04 (2)	0.02 (1)
	putatus		0.02 (2)	
LASIINI				
Paratrechina	**1**	0.76 (617)		
	5	0.40 (276)	0.36 (686)	0.90 (2,950)
	6	0.82 (721)	0.68 (668)	0.02 (2)
	8		0.72 (936)	0.78 (876)
	9		0.04 (51)	
	10	0.12 (10)		
PLAGIOLEPIDINI				
Plagiolepis	**3**	0.02 (1)	0.14 (59)	0.34 (24)
MYRMICINAE				
CREMATOGASTRINI				
Crematogaster	**3**	0.04 (3)	0.12 (15)	0.06 (3)
	8	0.24 (40)	0.04 (2)	
	9	0.10 (7)	0.08 (27)	
	12			0.02 (1)
	schenki			0.04 (2)
DACETONINI				
Kyidris	**1**		0.46 (927)	0.08 (22)
Smithistruma	6	0.02 (2)	0.02 (1)	0.02 (1)
	7	0.02 (1)	0.20 (43)	
Strumigenys	**1**	0.26 (132)	0.62 (564)	0.60 (224)
	13	0.44 (91)	0.04 (9)	0.02 (1)
	14	0.28 (37)	0.42 (159)	0.04 (5)
	19		0.04 (2)	0.02 (1)
	22	0.36 (79)	0.48 (88)	0.12 (8)
	23			0.12 (6)
	24	0.50 (104)	0.84 (370)	
	25	0.24 (21)	0.02 (1)	0.20 (21)
	26	0.20 (31)	0.32 (56)	0.42 (62)
	27	0.06 (10)	0.38 (89)	
	28	0.04 (10)	0.12 (9)	0.22 (19)
	29		0.02 (2)	0.90 (246)

TABLE 4-4. *Continued.*

Genus	Species	25 m	425 m	825 m
	30			0.14 (20)
	37		0.04 (2)	
	51			0.04 (2)
	52			0.06 (5)
	53	0.16 (30)	0.24 (54)	
	55			0.08 (5)
PHEIDOLINI				
Aphaenogaster	*gonacantha*		0.38 (33)	
Pheidole	**13**			0.06 (6)
	20	0.06 (8)	0.68 (866)	
	23	0.02 (2)		
	41			0.06 (67)
	43	0.50 (438)	0.38 (92)	
	44	0.52 (789)	0.58 (847)	0.28 (156)
	49			0.04 (204)
	50	0.12 (66)	0.28 (311)	0.36 (104)
	52			0.02 (7)
	53	0.28 (228)	0.02 (2)	0.18 (191)
	54			0.02 (16)
	58		0.10 (145)	0.52 (571)
	62			0.48 (275)
	63			0.06 (7)
	64			0.20 (96)
	65			0.06 (87)
	66			0.02 (3)
	67			0.04 (34)
	68	0.78 (8,083)	0.96 (10,045)	
	69	0.40 (134)	0.48 (355)	
	70	0.20 (140)	0.22 (246)	
	71	0.50 (951)	0.04 (23)	
	72		0.02 (25)	
	73	0.34 (73)	0.08 (14)	
	74	0.02 (1)		
	oswaldi	0.20 (146)	0.42 (636)	
	spinosa	0.48 (302)	0.46 (180)	
	veteratrix			0.94 (779)
PHEIDOLOGETONINI				
Oligomyrmex	**3**	0.22 (39)		0.52 (210)
	6	0.12 (30)	0.06 (60)	0.42 (577)
SOLENOPSIDINI				
Monomorium	2			0.14 (11)
	5		0.02 (47)	0.02 (1)
	7		0.48 (220)	0.68 (427)
	14	0.42 (81)	0.58 (259)	
	23		0.14 (25)	0.50 (301)
	24			0.22 (81)
	26	0.02 (1)	0.20 (48)	
	28			0.12 (33)
	33			0.18 (23)
	34			0.66 (1,707)
	36	0.08 (10)	0.46 (212)	0.02 (4)
	38			0.02 (2)
	39	0.32 (371)	0.04 (17)	0.64 (1,012)
	41		0.14 (62)	
	42	0.02 (2)		0.06 (25)

TABLE 4-4. *Continued.*

Genus	Species	25 m	425 m	825 m
TETRAMORIINI				
Tetramorium	**6**		0.02 (1)	0.14 (21)
	7	0.02 (2)		0.02 (5)
	16	0.12 (16)	0.32 (98)	
	21	0.02 (1)	0.12 (10)	
	23	0.52 (110)	0.24 (35)	
	24			0.24 (43)
	25		0.02 (1)	0.10 (6)
	26		0.08 (5)	
	29			0.02 (2)
	34	0.36 (64)	0.12 (12)	
	35	0.04 (3)		
	36		0.40 (261)	
	37		0.18 (85)	0.42 (149)
	39			0.08 (10)
	40	0.40 (181)	0.34 (49)	0.02 (2)
	41	0.56 (104)	0.52 (87)	
	42		0.04 (2)	
	43	0.06 (25)	0.02 (2)	
	andrei	0.64 (285)	0.08 (7)	0.04 (3)
	dysalum	0.28 (45)	0.04 (5)	0.02 (1)
	electrum			0.04 (2)
	marginatum		0.74 (366)	0.02 (2)
	naganum	0.18 (21)	0.02 (1)	0.28 (26)
	tosii	0.10 (5)	0.30 (56)	
INCERTAE SEDIS				
Undescribed genus	2			0.80 (221)
	3	0.54 (120)	0.32 (83)	
PONERINAE				
AMBLYOPONINI				
Amblyopone	1		0.02 (1)	
	4			0.04 (3)
Mystrium	**3**			0.06 (3)
	4	0.50 (104)	0.20 (18)	
	5		0.02 (2)	
Prionopelta	1	0.16 (44)	0.10 (82)	0.14 (33)
	4			0.76 (228)
	5	0.08 (4)	0.24 (25)	
ECTATOMMINI				
Discothyrea	3			0.12 (22)
	5		0.02 (1)	0.08 (27)
	6	0.02 (1)		
	7		0.02 (1)	
Proceratium	2	0.10 (5)	0.02 (1)	
	diplopyx			0.06 (3)
PONERINI				
Anochetus	*grandidieri*	0.34 (71)	0.24 (97)	0.02 (14)
Hypoponera	**22**			0.04 (8)
	26		0.02 (1)	0.64 (181)
	29			0.02 (1)
	32	0.38 (60)	0.46 (260)	
	33	0.68 (216)	0.06 (6)	
	36	0.34 (76)	0.68 (310)	
	38			0.32 (87)
	39			0.88 (986)
	43	0.12 (21)	0.06 (25)	

TABLE 4-4. *Continued.*

Genus	Species	25 m	425 m	825 m
	44	0.20 (103)	0.38 (180)	
	46	0.06 (12)	0.06 (3)	0.18 (38)
	47		0.18 (79)	0.46 (185)
	48			0.02 (2)
	49			0.04 (5)
	50			0.04 (2)
	51		0.12 (18)	
	52	0.02 (1)		
	sakalava	0.06 (6)	0.08 (10)	0.02 (3)
Leptogenys	4		0.02 (2)	
	5			0.02 (9)
	6			0.04 (3)
	7			0.02 (1)
	11			0.02 (1)
Odontomachus	*coquereli*		0.02 (1)	0.02 (1)
Pachycondyla	**1**			0.14 (20)
	2	0.20 (15)	0.14 (10)	
	cambouei	0.08 (5)	0.12 (7)	0.20 (15)
	perroti	0.04 (4)		
Ponera	1	0.06 (9)	0.34 (70)	

* The number of individual workers collected is given in parentheses. Species listed in boldface type were also collected in the RS d'Anjanaharibe-Sud (Table 4-3).
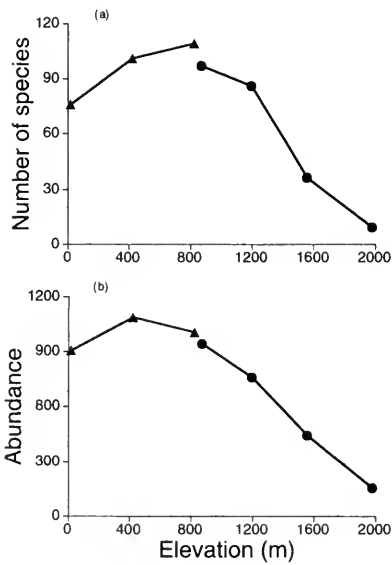
FIG. 4-2. Number of ant species (**a**) and total abundance (**b**) as a function of elevation. Abundance is measured as the total number of stations at which each species was collected (see text for details). Data are from pitfall and mini-Winkler samples from the Masoala Peninsula (▲, 25–825 m) and the RS d'Anjanaharibe-Sud (●, 875–1985 m).

also a significant relationship between observed species richness and abundance, measured as the total number of stations at which each species was collected (Fig. 4-5; $r^2 = .94$, $p < 0.0005$). The relationship between species richness and elevation, however, cannot be attributed to differences in abundance. Observed species accumulation curves based on abundance, measured as the total number of stations at which each species was collected (not number of stations sampled), for each elevation are not identical (Fig. 4-6). Species-rich sites have a higher rate of discovery of new species than species-poor sites. Thus, comparisons of observed species richness across sites were not confounded by the potential sampling-induced bias of differences in abundance.

Efficacy of Inventory Methods

For all elevations sampled, species accumulation curves appear to be leveling off toward an asymptote and thus reflect the actual number of species present in the area sampled along the 250 m transect at each elevation site. Additional collecting methods, or a survey in a different area or season at the same elevation, would most likely result in the collection of additional species. The ICE- and jackknife-estimated species richnesses are almost identical for each elevation when all

TABLE 4-5. Total number of species and relative importance (%) of each subfamily for pitfall and leaf litter collections on the Masoala Peninsula and in the RS d'Anjanaharibe-Sud (general collections are excluded).

Altitude (m)	Cerap	Dolichod	Form	Pon	Myrm	P/M[†]
			Subfamily*			
Masoala						
25	1 (1%)	0	7 (9%)	18 (24%)	50 (66%)	0.36
425	2 (2%)	1 (1%)	12 (12%)	24 (24%)	62 (62%)	0.39
825	7 (6%)	1 (1%)	12 (11%)	26 (23%)	63 (56%)	0.41
All elevations	**7 (4%)**	**1 (1%)**	**17 (10%)**	**44 (26%)**	**98 (59%)**	**0.45**
RS d'Anjanaharibe-Sud						
875	6 (6%)	0	9 (9%)	31 (32%)	51 (53%)	0.61
1200	5 (6%)	1 (1%)	12 (14%)	19 (22%)	49 (57%)	0.39
1280	3 (6%)	0	4 (8%)	14 (26%)	32 (60%)	0.44
1565	2 (4%)	0	8 (16%)	10 (20%)	30 (60%)	0.33
1985	0	0	2 (22%)	1 (11%)	6 (66%)	0.17
All elevations	**12 (7%)**	**1 (1%)**	**18 (10%)**	**50 (28%)**	**99 (55%)**	**0.51**

* Cerap = Cerapachyinae; Dolichod = Dolichoderinae; Form = Formicinae; Pon = Ponerinae; and Myrm = Myrmicinae.
[†] P/M = taxonomic ratio of species in the Ponerinae and Myrmicinae.

stations are pooled (Figs. 4-3, 4-4). In some cases (e.g., Fig. 4-3b, d), the ICE method was less sensitive to sample size than the jackknife method. The precision of these estimators is difficult to determine because a site would need to be exhaustively surveyed to produce a complete species list. Nevertheless, these results show that the inventory techniques used in this study provide sufficient sampling for statistical estimation, comparison of species richness, and comparison of faunal similarity and species turnover.

An alternative approach to evaluating the question of efficacy is to ask what minimum number of collections is necessary to provide the same relative ranking of species richness among elevations, as shown in Figure 4-2. Do pitfall samples alone show the same midelevation peak? No; within the Masoala Peninsula locality, the 825 m site had the lowest number of species recorded from pitfalls. Species accumulation curves for pitfall samples are still rising rapidly after 50 samples, which suggests that pitfall samples in this study do not provide sufficient sampling for comparison among elevations. Alternatively, it is pos-

TABLE 4-6. Number of species collected and first-order jackknife and ICE estimates of total species richness (with 95% confidence intervals) based on pitfall and leaf litter transects on the Masoala Peninsula and in the RS d'Anjanaharibe-Sud.*

Altitude (m)	Observed	ICE	95% CI[†]	Jackknife	95% CI[†]
Masoala					
25	76	84.8	0.26	87.8	0.77
425	101	120.3	0.38	122.6	0.93
825	109	141.7	0.47	139.4	1.04
All elevations	**167**	**187.7**	**0.35**	**193.8**	**1.01**
RS d'Anjanaharibe-Sud					
875	97	126.7	0.68	122.5	1.12
1200	86	97.4	0.27	101.7	0.71
1280	52	63.4	0.29	65.5	0.57
1565	50	66.3	0.34	63.7	0.62
1985	9	11.3	0.16	11.0	0.27
All elevations	**179**	**209.9**	**0.03**	**214.3**	**1.23**

* Statistics are given for each altitude and for all elevations combined. The observed and estimated species richness values for 1280 m are based on 26 leaf litter and the first 26 pitfall trap samples.
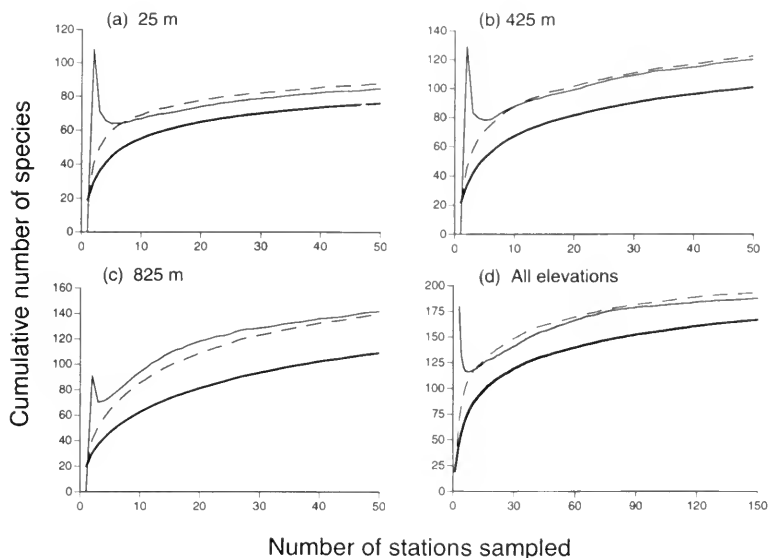[†] CI = confidence interval.
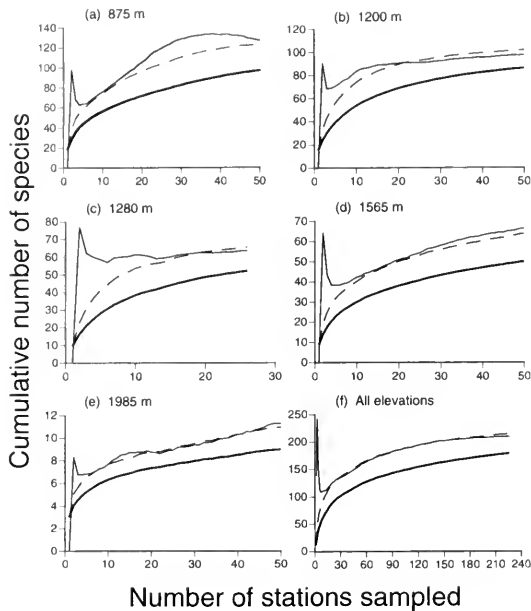
FIG. 4-3. Assessment of leaf litter ant sampling technique for each elevation (a–e) and for all elevations combined (f) in the RS d'Anjanaharibe-Sud. The lower species accumulation curve (thick line) in each chart plots the observed number of species as a function of the number of stations sampled. The upper curves display the nonparametric first-order jackknife (dashed line) and the ICE (thin line) estimated total species richness based on successively larger number of samples from the data set (Heltshe & Forrester, 1983; Lee & Chao, 1994). Curves are plotted from the means of 100 randomizations of sample accumulation order.

TABLE 4-8. Beta-1 (above the diagonal) and beta-2 (below the diagonal) diversity values of each pair of altitude sites.*

RS d'Anjanaharibe-Sud[†]

Elevation	875 m	1200 m	1565 m	1985 m
875 m	—	**0.563**	0.838	0.981
1200 m	**0.474**	—	**0.618**	0.979
1565 m	0.392	**0.280**	—	**0.967**
1985 m	0.082	0.093	**0.080**	—

Masoala Pensinula[‡]

Elevation	25 m	425 m	825 m
25 m	—	**0.266**	0.643
425 m	**0.110**	—	**0.514**
825 m	0.394	**0.459**	—

Between the RS d'Anjanaharibe-Sud (875 m) and the Masoala Peninsula (825 m)

	875 and 825 m	All elevations
β-1	0.553	0.562
β-2	0.486	0.506

* Higher values represent greater species turnover. Values in boldface type represent comparisons of altitudinally adjacent transects.
[†] Overall beta-1 diversity was 2.050; beta-2 diversity was 0.856.
[‡] Overall beta-1 diversity was 0.752; beta-2 diversity as 0.532.

TABLE 4-7. Two measurements of faunal similarity between elevational zones and regions sampled.*

RS d'Anjanaharibe-Sud

Elevation	875 m	1200 m	1565 m	1985 m
875 m	—	**0.280**	0.089	0.010
1200 m	**0.272**	—	**0.236**	0.011
1565 m	0.093	**0.198**	—	**0.093**
1985 m	0.000	0.002	**0.228**	—

Masoala Peninsula

Elevation	25 m	425 m	825 m
25 m	—	**0.580**	0.217
425 m	**0.659**	—	**0.321**
825 m	0.170	**0.270**	—

Between the RS d'Anjanaharibe-Sud (875 m) and the Masoala Peninsula (825 m)

	875 and 825 m	All elevations
Jaccard Index	0.288	0.280
Morisita Index	0.322	—

* Above the diagonal is the Jaccard Index of similarity (presence and absence data), and below the diagonal, the simplified Morisita Index of similarity (abundance data; Horn, 1966). Higher values represent greater similarity. Values in boldface type represent comparisons of altitudinally adjacent transects.

FIG. 4-4. Assessment of leaf litter ant sampling technique for each elevation (**a–c**) and for all elevations combined (**d**) on the western Masoala Peninsula. The lower species accumulation curve (thick line) in each chart plots the observed number of species as a function of the number of stations sampled. The upper curves display the nonparametric first-order jackknife (dashed line) and ICE (thin line) estimated total species richness based on successively larger number of samples from the data set (Heltshe & Forrester, 1983; Lee & Chao, 1994). Curves are plotted from the means of 100 randomizations of sample accumulation order.

sible that pitfalls sample a different subset of the ant fauna that does not show a midelevation peak. For mini-Winkler samples, the same relative ranking in observed species richness was reached and maintained after 25 samples. A lower number of leaf litter samples will produce a more incomplete species list necessary for species turnover and faunal similarity studies, but fewer samples may be appropriate for addressing questions on the relative ranking of species richness.

Comparisons with Other Faunas

The ant fauna of Madagascar is incompletely known, with two-thirds of the 1,000 estimated species on the island thought to be undescribed (Fisher, 1996b, 1997). No previous records exist for ants collected in the RS d'Anjanaharibe-Sud. Mocquery collected in the late 19th century near the Baie d'Antongil, approximately 90 km south-southeast of the RS d'Anjanaharibe-Sud (Emery,

TABLE 4-9. Number of species shared between elevations from the Masoala Peninsula (25–825 m) and the RS d'Anjanaharibe-Sud (875–1985 m).*

Elevation	25	425	825	875	1200	1565	1985
25	**6 (8)**						
425	65	**13 (13)**					
825	33	51	**39 (36)**				
875	31	40	46	**37 (38)**			
1200	25	31	42	40	**18 (21)**		
1565	10	10	11	12	26	**16 (32)**	
1985	1	1	1	1	1	5	**4 (44)**

* The 1280 m site is excluded. The number and percentage (in parentheses) of species unique to an elevation are presented along the diagonal. The number of species unique to 875 m was calculated in the absence of the 825 m data. Likewise, 875 m data were not used in calculating species unique to the 825 m site.
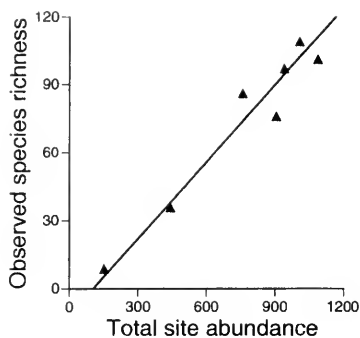
FIG. 4-5. Number of total species at each elevation from the RS d'Anjanaharibe-Sud and the western Masoala Peninsula plotted as a function of total abundance, which was measured as the total number of stations at which each species was collected ($r^2 = 0.94$, $P < 0.005$).

FIG. 4-6. Observed species richness accumulation curves for each elevation plotted as a function of abundance, which was measured as the total number of stations at which each species was collected. Curves are plotted from the means of 100 randomizations of sample accumulation order.

1899), and provided important collections for the region (Wheeler, 1922). Subsequent collections in the Baie d'Antongil region have been made by Ward and Alpert.

For the island of Madagascar, 90% of the valid specific and subspecific ant taxa are endemic (Fisher, 1996b, 1997). In the RS d'Anjanaharibe-Sud, 100% of the ants collected are thought to be endemic to Madagascar, except for *Serrastruma ludovici*, which is widespread in Africa and is also known from Mauritius (Bolton, 1983). On the Masoala Peninsula, the lowest elevations contained two tramp species. These tramp species were collected in open areas along sandy beaches (*Tetramorium bicarinatum*) and disturbed forest areas (*Technomyrmex albipes*) and were not encountered in the undisturbed forest transects. We do not know how susceptible the forest ant assemblages of Madagascar are to invasion by tramp species, especially *Technomyrmex albipes*. In the RS de Nosy Mangabe, field observations by P. S. Ward (pers. comm.) suggest that ant diversity is depressed in areas occupied by *Technomyrmex albipes*. Monitoring efforts should be directed at measuring the advance of this species from disturbed habitats to relatively undisturbed habitats. As fragmentation of the remaining forest habitats increases in Madagascar, their susceptibility to invasion will probably increase.

The high similarity of the ant fauna of the 875 m site in the RS d'Anjanaharibe-Sud and 825 m site on the Masoala Peninsula (Table 4-7) suggests a shared history. The two sites are located approximately 110 km apart and are connected by a

band of midelevation forest. Even given this similarity, many differences in species assemblages still exist between the two sites (Tables 4-1, 4-3). The endemic genus *Eutetramorium* was abundant in general collections at 875 m in the RS d'Anjanaharibe-Sud (*E. mocquerysi*) but was not collected on the western side of the Masoala Peninsula, although this species is known from the RNI de Marojejy and on the eastern side of Masoala Peninsula (Alpert & Rabeson, in press). An undescribed endemic myrmicine genus was abundant at both localities, but different species were found at each.

The relative prevalences of species from the subfamilies Ponerinae and Myrmicinae are similar in the RS d'Anjanaharibe-Sud (28% and 55%, respectively) and on the Masoala Peninsula (26% and 59%, respectively) (Table 4-5). The Ponerinae/Myrmicinae ratio (0.51 and 0.45, respectively) is greater than that found for the RNI d'Andringitra (0.35; Fisher, 1996a) and other tropical sites in sub-Saharan Africa, Central America, and Australia (Table 8-6 in Fisher, 1996a). Previous results suggested that a 1:3 ratio of Ponerinae to Myrmicinae could be used to interpolate the species richness of one subfamily from the other (Fisher, 1996a). Because of the differences in ratios among localities and elevations, the current study suggests that the 1:3 taxonomic ratio is not universal. The application of taxonomic ratios to estimating ant species richness in Madagascar may not be appropriate and will require, at a minimum, region- and elevation-specific calibrations.

Acknowledgments

Literature Cited

ALPERT, G. D., AND P. RABESON. In press. *Eutetramorium*, a rare ant genus endemic to Madagascar (Hymenoptera: Formicidae). Psyche.

BESUCHET, C., D. H. BURCKHARDT, AND I. LOBL. 1987. The "Winkler/Moczarski" eclector for fungus and litter Coleoptera. The Coleopterists Bulletin, **41:** 393–394.

BOLTON, B. 1983. The Afrotropical dacetine ants (Formicidae). Bulletin of the British Museum (Natural History), Entomology Series, **46:** 267–416.

BROWN, W. L., JR. 1973. A comparison of the Hylean and Congo–West African rain forest ant faunas, pp. 161–185. *In* Meggers, B. J., E. S. Ayensu, and W. D. Duckworth, eds., Tropical Forest Ecosystems in Africa and South America: A Comparative Review. Smithsonian Institution Press, Washington, D.C.

CHAZDON, R. L., R. K. COLWELL, J. S. DENSLOW, AND M. R. GUARIGUATA. In press. Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forests of NE Costa Rica. *In* Dallmeier, F., ed., Proceedings of the SI/MAB International Symposium on Measuring and Monitoring Forest Biological Diversity: The International Network of Biodiversity Plots. Smithsonian Institution Press, Washington, D.C.

COLWELL, R. K., AND J. A. CODDINGTON. 1994. Estimating terrestrial biodiversity through extrapolation. Philosophical Transactions of the Royal Society of London, Series B, **345:** 101–118.

EMERY, C. 1899. Formiche di Madagascar raccolte dal Sig. A. Mocquerys nei pressi della Baia di Antongil (1897–1898). Bullettino della Società Entomologica Italiana, **31:** 263–290.

FISHER, B. L. 1996a. Ant diversity patterns along an elevational gradient in the Réserve Naturelle Intégrale d'Andringitra, Madagascar, pp. 93–108. *In* Goodman, S. M., ed., A floral and faunal inventory of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: With reference to elevational variation. Fieldiana: Zoology, n.s., **85:** 1–319.

———. 1996b. Origins and affinities of the ant fauna of Madagascar, pp. 457–465. *In* Lourenco, W. L., ed., Biogéographie de Madagascar. Editions ORSTOM, Paris.

———. 1997. Biogeography and ecology of the ant fauna of Madagascar (Hymenoptera: Formicidae). Journal of Natural History, **31:** 269–302.

FISHER, B. L., AND S. RAZAFIMANDIMBY. 1997. Les Fourmis (Hymenoptera: Formicidae), pp. 105–111. *In* Goodman, S. M., and O. Langrand, eds., Inventaire biologique forêt de Vohibasia et d'Isoky-Vohimena. Série Sciences biologiques. N°. Spéciale. World Wide Fundfer Nature, Centre d'Information et de Documentation Scientifique et Technique, Antananarivo.

GASTON, J. K., T. R. NEW, AND M. J. SAMWAYS, EDS. 1993. Perspectives on insect conservation. Intercept Ltd., Andover, UK, 250 pp.

HARRISON, S., S. J. ROSS, AND J. H. LAWTON. 1992. Beta diversity on geographic gradients in Britain. Journal of Animal Ecology, **61:** 151–158.

HELTSHE, J. F., AND N. E. FORRESTER. 1983. Estimating species richness using the jackknife procedure. Biometrics, **39:** 1–11.

HORN, H. S. 1966. Measurement of 'overlap' in comparative ecological studies. American Naturalist, **100:** 419–424.

LEE, S.-M., AND A. CHAO. 1994. Estimating population size via sample coverage for closed capture-recapture models. Biometrics, **50:** 88–97.

MAGURRAN, A. E. 1988. Ecological Diversity and Its Measurement. Princeton University Press, Princeton, N.J., 179 pp.

OLSON, D. M. 1994. The distribution of leaf litter invertebrates along a Neotropical altitudinal gradient. Journal of Tropical Ecology, **10:** 129–150.

PALMER, M. W. 1995. How should one count species? Natural Areas Journal, **15:** 124–135.

PULLIAM, H. R. 1988. Source, sinks, and population regulation. The American Naturalist, **132:** 652–661.

RAHBEK, C. 1995. The elevational gradient of species richness: A uniform pattern? Ecography, **18:** 200–205.

———. 1997. The relationship between area, elevation, and regional species richness in Neotropical birds. The American Naturalist, **149:** 875–902.

ROSENZWEIG, M. L., AND Z. ABRAMSKY. 1993. How are diversity and productivity related?, pp. 52–65. *In* Ricklefs, R., and D. Schluter, eds., Species Diversity in Ecological Communities: Historical and Geographical Perspectives. University of Chicago Press, Chicago.

STEVENS, G. C. 1989. The latitudinal gradient in geographical range: How so many species coexist in the tropics. The American Naturalist, **133:** 240–256.

———. 1992. The elevational gradient in altitudinal range: An extension of Rapoport's latitudinal rule to altitude. The American Naturalist, **140:** 893–911.

WHEELER, W. M. 1922. Ants of the American Museum Congo expedition: A contribution to the myrmecology of Africa. IX. A synonymic list of the ants of the Malagasy region. Bulletin of the American Museum of Natural History, **45:** 1005–1055.

WHITTAKER, R. M. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs, **30:** 279–338.

WOLDA, H. 1981. Similarity indices, sample size and diversity. Oecologia, **50:** 296–302.

Chapter 5

Description of a New Species of Scorpion from the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar

Wilson R. Lourenço[1]

Abstract

Among the few scorpion specimens collected in the Réserve Spéciale d'Anjanaharibe-Sud was a new species belonging to the enigmatic genus *Microcharmus* Lourenço, 1995 (Scorpiones, Buthidae, Microcharminae). At the two sites where the new species was found, it was associated with immature forms of *Grosphus madagascariensis* (Gervais). With the description of *Microcharmus fisheri*, new species, the total number of species known for this genus is five, all of which occur only in northern Madagascar.

Résumé

Parmi quelques scorpions collectés dans la Réserve Spéciale d'Anjanaharibe-Sud, une nouvelle espèce appartenant au très énigmatique genre *Microcharmus* Lourenço, 1995 (Scorpiones, Buthidae, Microcharminae) a été trouvée. Elle est décrite à présent. Dans les deux sites de collecte de la nouvelle espèce, celle-ci se trouvait associée avec des formes immatures de *Grosphus madagascariensis* (Gervais). Avec la description de *Microcharmus fisheri,* nouvelle espèce, le nombre total d'espèces s'élève à cinq.

Introduction

Few scorpions were collected during the inventory of the Réserve Spéciale d'Anjanaharibe-Sud. However, the use of mini-Winkler extraction techniques (see Chapter 4) led to the discovery of a new species of scorpion belonging to the enigmatic genus *Microcharmus* Lourenço, 1995 (Buthidae, Microcharminae). When this genus was described 2 years ago (Lourenço, 1995), it was known only by the type species, *M. cloudsleythompsoni*. Subsequently, a second species, *M. hauseri* Lourenço, 1996 (Lourenço, 1996a), was described from Nosy Be. Finally, with the recent publication of the scorpion volume in the *Faune*

de Madagascar series, two more species were added to the genus *Microcharmus*: *M. sabineae* and *M. jussarae* (Lourenço, 1996b). Including the new species described herein, the total number of species of *Microcharmus* is now five.

Microcharmus fisheri Lourenço, new species (Fig. 5-1)

Holotype (male) and allotype (female): Madagascar, 9.2 km SSW of Befingotra, Réserve Spéciale d'Anjanaharibe-Sud, 14°45′S, 49°28′E (1200 m), 9 November 1994, B. L. Fisher. Two paratypes (one male and one female): Madagascar, 6.5 km SSW of Befingotra, Réserve Spéciale d'Anjanaharibe-Sud, 14°45′S, 49°30′E (875 m, from sifted litter, leaf mold rotten wood in mon-

[1] Laboratoire de Zoologie (Arthropodes), Muséum National d'Histoire Naturelle, 61, rue de Buffon, 75005, Paris, France.
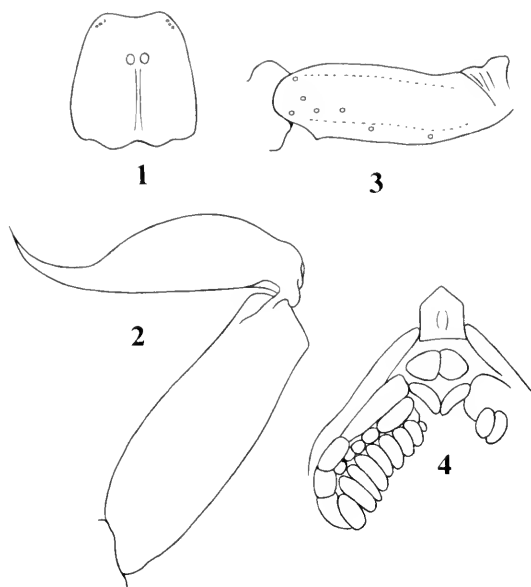
FIG. 5-1. **1–3**, *Microcharmus fisheri*, male holotype: carapace (**1**), metasomal segment V and telson, lateral view (**2**), and femur, dorsal view, showing A-α trichobothrial configuration (**3**). **4**, *Microcharmus fisheri*, female allotype: ventral region, showing sternum, genital operculum, and pectines.

tane rain forest), 19 October 1994, B. L. Fisher (1070). At both sites where the new species was collected, it was associated with immature forms of *Grosphus madagascarienis* (Gervais, 1844).

Holotype, allotype, and one paratype (female) deposited in the Field Museum of Natural History. One paratype (male) deposited in the Muséum National d'Histoire Naturelle, Paris.

Etymology: Patronym in honor of Brian L. Fisher, who collected the specimens.

Diagnosis

The new species differs from *Microcharmus cloudsleythompsoni*, *M. sabineae*, and *M. jussarae* by possessing a variegated pattern of pigmentation, which is also known in *M. hauseri*. *Microcharmus fisheri* is distinguished from *M. hauseri* by differences in the pattern of pigmentation, mainly of the chelicerae and telson (see key).

Key to the species of *Microcharmus*

1. Three pairs of lateral eyes 2
    Two pairs of lateral eyes . . . . *M. sabineae*

TABLE 5-1. Measurements (in mm) of the male holotype of *M. fisheri*, new species.

Carapace	
Length	1.6
Anterior width	1.1
Posterior width	1.8
Metasomal segment I	
Length	0.8
Width	1.0
Metasomal segment V	
Length	2.1
Width	0.8
Depth	0.8
Vesicle	
Width	0.5
Depth	0.5
Pedipalp	
Femur length	1.2
Tibia length	1.8
Chelae length	2.4
Movable finger	
Length	1.6

2. General coloration very pale, with only vestigal spots; spiracles semioval or oval 3
    General coloration yellowish with several brownish spots over the body legs and pedipalps, giving a general variegated appearance; spiracles semilinear .4
3. Pectinial tooth count from 9 to 12 . . . .
    . . . . *M. cloudsleythompsoni*
    Pectinial tooth count from 7 to 9 . . . .
    . . . . *M. jussarae*
4. Chelicerae recovered with variegated brownish spots; telson yellowish without spots . . . . .
    . . . . *M. hauseri*
    Chelicerae yellowish with some diffuse brownish spots anteriorly; telson yellowish with the dorsal surface brownish and large brownish spots laterally . . . .*M. fisheri*

Description Based on Male Holotype
(measurements presented in Table 5-1)

COLORATION—Basically yellowish brown, symmetrically marbled with dark reddish brown, producing an overall variegated appearance. Prosoma: carapace yellowish and heavily spotted; eyes surrounded by black pigment. Mesosoma: yellowish with confluent brown stripes, producing a variegated appearance. Venter yellowish with three longitudinal brownish strips over the sternites.
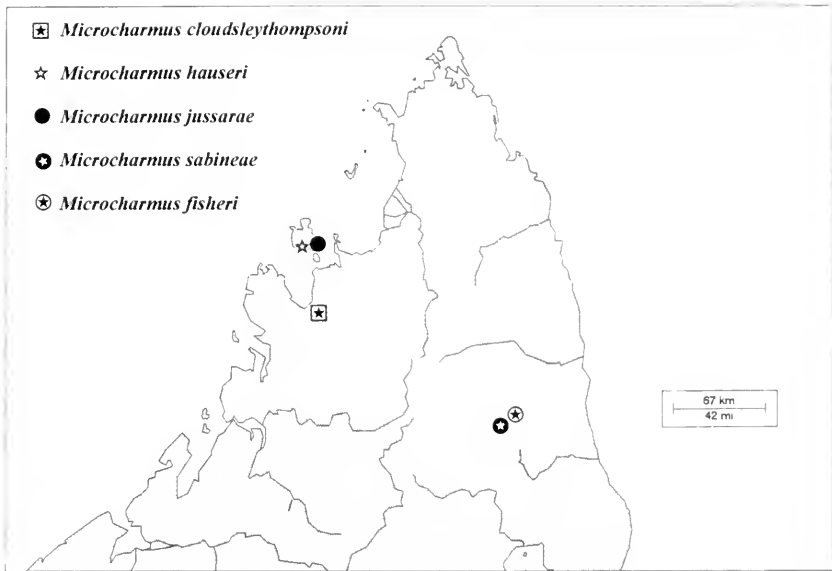
FIG. 5-2. Map of northern Madagascar showing the type localities for the known species of the genus *Microcharmus*.

Metasoma: segments I–III yellowish; IV and V reddish yellow, with numerous brown spots. Telson: Vesicle yellowish with the dorsal surface brownish and large brownish spots laterally. Chelicerae yellowish with some diffuse brownish spots anteriorly; fingers light reddish. Pedipalps: yellowish with brown spots on femur and tibia; chelae yellowish; fingers brownish at the base. Legs yellowish with diffuse brownish spots.

MORPHOLOGY—Carapace slightly granular; anterior margin with a slight median concavity. Anterior median, superciliary, and posterior median keels not strongly developed. All furrows moderate to weak. Median ocular tubercle distinctly anterior to the center portion of the carapace; median eyes separated by one ocular diameter. Three pairs of lateral eyes. Sternum subpentagonal to pentagonal. Mesosoma: tergites moderate to slightly granular. Median keel moderate in all tergites; vestigial on VII. Tergite VII pentacarinate. Venter: genital operculum divided longitudinally. Pectines: pectinal tooth count 10–10; basal middle lamellae of the pectines not dilated; fulcra absent. Sternites almost smooth with semioval to semilinear stigmata; VII without keels. Metasoma: segments I–III with 10 keels, crenulate. Segment IV with 8 keels, crenulate. Intercarinal spaces slightly granular. Segment V with only vestigial keels, round. Telson smooth and flattened, without keels and with a short and moderately curved aculeus; subaculear tooth absent. Cheliceral dentition char-acteristic of the family Buthidae (Vachon, 1963); however, distinctly smaller than the typical condition in this family. Pedipalps: femur pentacarinate, slightly crenulate; tibia and chelae with some vestigial keels, slightly crenulate; all faces slightly granular. Movable fingers with 7–8 semioblique rows of granules; accessory granules absent. Trichobothriotaxy; orthobothriotaxy A-α (Vachon, 1973, 1975). Legs: tarsus with very numerous fine setae ventrally. Tibial spurs moderately developed.

VARIATION—Coloration, pigmentation, and morphology of allotype similar to that of the holotype male. Smaller pectines; tooth count 8–8; basal middle lamellae not dilated. Paratypes: tooth count 10–10 (male) and 8–8 (female).

Biogeographical Remark

All of the described species of the genus *Microcharmus* are known only from the northern portion of Madagascar (Fig. 5-2). This genus shares close affinities with elements of the scorpion fauna of the Oriental region, that is, Sri Lanka and India (Lourenço, 1996c).

Literature Cited

LOURENÇO, W. R. 1995. Description de trois nouveaux genres et de quatre nouvelles espèces de Scorpions

Buthidae de l'île de Madagascar. Bulletin Muséum National d'Histoire Naturelle, Paris, quatrième séries, **17**(1–2): 95–106.

———. 1996a. *Microcharmus hauseri*, nouvelle espèce de Scorpion de Madagascar (Scorpiones, Buthidae). Revue Suisse Zoologie, **103**(2): 319–322.

———. 1996b. Scorpions (Chelicerata, Scorpiones), No. 87. *Faune de Madagascar*. Muséum National d'Histoire Naturelle, Paris, 102 pp.

———. 1996c. Origins and affinities of the scorpion fauna of Madagascar, pp. 441–455. *In* Lourenço, W. R., ed., Biogéographie de Madagascar. Edition de l'Orstom, Paris, 588 pp.

VACHON, M. 1963. De l'utilité, en systématique, d'une nomenclature des dents des chélicères chez les Scorpions. Bulletin Muséum National d'Histoire Naturelle, Paris, deuxième séries, **35**(2): 161–166.

———. 1973. Etude des caractères utilisés pour classer les families et les genres de Scorpions (Arachnides). 1. La trichobothriotaxie en arachnologie. Sigles trichobothriaux et types de trichobothriotaxie chez les Scorpions. Bulletin Muséum National d'Histoire Naturelle, Paris, troisième séries, no. 140, Zoologie, **104**: 857–958.

———. 1975. Sur l'utilisation de la trichobothriotaxie du bras des pédipalpes des Scorpions (Arachnides) dans le classement des genres de la famille des Buthidae Simon. Compte Rendus del' Académie des Sciences, Paris, série D, **281**: 1597–1599.

Chapter 6

Parasitic and Commensal Arthropods of Some Birds and Mammals of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar

Barry M. OConnor[1]

Abstract

Examination of 97 specimens representing 21 species of mammals and 15 specimens representing seven species of birds collected in the Réserve Spéciale (RS) d'Anjanaharibe-Sud yielded numerous collections of parasitic and commensal arthropods. All host species and most host individuals harbored arthropod associates. Preliminary identifications of 25 families of mites (Acari), as well as parasitic insects belonging to the orders Diptera, Siphonaptera, and Phthiraptera, are reported. The mite families Hypoderatidae, Gastronyssidae, and Rosensteiniidae are reported from Madagascar for the first time. The ectoparasite fauna of RS d'Anjanaharibe-Sud is generally similar in its overall makeup to that of the Réserve Naturelle Intégrale d'Andringitra.

Résumé

L'examen de 97 spécimens appartenant à 21 espèces de mammifères et 15 spécimens appartenant à sept espèces d'oiseaux collectés dans la Réserve Spéciale d'Anjanaharibe-Sud a permis la collecte de nombreux arthropodes parasites et commensaux. Toutes les espèces hôtes et la plupart des individus ont révélés la présence d'arthropodes associés. Des travaux préliminaires ont permis l'identification de 25 familles de mites (Acari), de même que des insectes parasites appartenant à l'ordre des Diptera, des Siphonaptera, et des Phthiraptera. La présence des familles de mites des Hypoderatidae, des Gastronyssidae et des Rosensteiniidae est reportée pour la première fois de Madagascar. La faune ectoparasite d'Anjanaharibe-Sud est généralement similaire à celle trouvée au sein de la Réserve Naturelle Intégrale d'andringitra.

Introduction

The parasitic and commensal arthropods associated with Madagascar's unique vertebrate fauna remain poorly studied. I recently reviewed the literature summarizing this parasite fauna and provided preliminary lists of some families and genera of mites and orders of insects associated with birds and mammals of the Réserve Naturelle Intégrale (RNI) d'Andringitra (OConnor, 1996). In this chapter I report the results of a similar survey conducted in the Réserve Spéciale (RS) d'Anjanaharibe-Sud.

[1] Museum of Zoology, University of Michigan, Ann Arbor, MI 48109 U.S.A.

Materials and Methods

A total of 97 specimens representing 21 species of mammals and 15 specimens representing seven species of birds collected in the RS d'Anjanaharibe-Sud were examined for parasites. Specimens were collected by S. M. Goodman and associates during a survey of this area in 1994. Specimens to be examined for parasites were kept separate from others during collecting, individually wrapped in cheesecloth, and fixed in formalin. The wrapped specimens were later transferred to 70% ethanol and loaned to my laboratory at the University of Michigan. There, each specimen was unwrapped and examined in detail under a dissecting microscope. Ectoparasites and commensals were removed with forceps and sorted by taxon and location on the host. The nasal passages of the hosts were flushed using a modification of the technique described by Yunker (1961) to remove upper respiratory endoparasites. Data for each collection of parasites from each host individual have been entered into a database maintained in the Insect Division of the Museum of Zoology, University of Michigan. In this system, each host specimen represents one lot of parasite specimens. Data captured for each lot include host identification, collection locality, date, collector, collector's field number, museum in which the host specimen is housed, museum catalog number of the host, and a catalog lot number for the collection. Each lot also includes individual sublots representing each sorted collection of parasites as noted above. The catalog lot number is stored with each collection of parasites and is printed on each parasite slide label, thus maintaining the connection between host and parasite specimens. The process of preparing specimens on microscope slides for final identification is continuing, with a large number of previously undescribed species expected.

The following list is a preliminary report of the results of this sampling. Because final identifications and descriptions of new taxa for most collections are still pending, I report here the parasite and commensal faunas for each host species, generally at the level of family or occasionally at the level of genus or species. For each host species, the number of individuals examined is indicated after the species name, and the number of host individuals harboring a particular arthropod taxon is listed after the taxon name if more than one host was examined.

Results

Class Mammalia

Order Insectivora

Family Tenrecidae

Microgale cowani (N = 12)
    Acari: Parasitiformes
        Ixodidae (7)
        Laelapidae (12)
        Pachylaelapidae (2)
    Acari: Acariformes
        Trombiculidae (10)
        Myobiidae
            Microgalobia sp. (7)
            Madamyobia sp. (7)
        Glycyphagidae (3)
        Atopomelidae
            Listrophoroides (*Alistrophoroides*) (9)
            Listrophoroides (*Madlistrophoroides*) (10)
        Sarcoptidae
            Notoedres (1)

Microgale dobsoni (N = 8)
    Acari: Parasitiformes
        Ixodidae (5)
        Laelapidae (8)
    Acari: Acariformes
        Trombiculidae (8)
        Myobiidae
            Microgalobia sp. (1)
        Glycyphagidae (5)
        Atopomelidae
            Listrophoroides (*Alistrophoroides*) (7)
            Listrophoroides (*Madlistrophoroides*) (6)

Microgale gymnorhyncha (N = 1)
    Acari: Parasitiformes
        Ixodidae
        Laelapidae
    Acari: Acariformes
        Trombiculidae

Microgale monticola (N = 3)
    Acari: Parasitiformes
        Ixodidae (2)
        Laelapidae (2)
    Acari: Acariformes
        Trombiculidae (2)
        Myobiidae
            Microgalobia sp. (1)

Atopomelidae
    Listrophoroides (*Alistrophoroides*) (3)
    Listrophoroides (*Madlistrophoroides*) (1)

Microgale parvula (N = 3)
  Acari: Parasitiformes
    Ixodidae (1)
  Acari: Acariformes
    Atopomelidae
      Listrophoroides (*Alistrophoroides*) (1)
      Listrophoroides (*Madlistrophoroides*) (1)

Microgale principula (N = 1)
  Acari: Parasitiformes
    Ixodidae
    Laelapidae
  Acari: Acariformes
    Glycyphagidae
    Atopomelidae
      Listrophoroides (*Alistrophoroides*)
      Listrophoroides (*Madlistrophoroides*)

Microgale soricoides (N = 3)
  Acari: Parasitiformes
    Laelapidae (2)
  Acari: Acariformes
    Trombiculidae (3)
    Glycyphagidae (2)
    Atopomelidae
      Listrophoroides (*Alistrophoroides*) (1)

Microgale talazaci (N = 3)
  Acari: Parasitiformes
    Ixodidae (3)
    Laelapidae (3)
  Acari: Acariformes
    Trombiculidae (3)
    Glycyphagidae (1)
    Atopomelidae
      Listrophoroides (*Alistrophoroides*) (2)
      Listrophoroides (*Madlistrophoroides*) (1)

Setifer setosus (N = 8)
  Acari: Parasitiformes
    Ixodidae (8)
    Laelapidae (8)
    Pachylaelapidae (1)
  Acari: Acariformes
    Trombiculidae (7)
    Glycyphagidae (5)
    Rosensteiniidae (5)
    Atopomelidae:
      Tenrecobia pauliana (Lawrence, 1955) (2)
  Insecta: Siphonaptera
    Unidentified family (3)

Order Chiroptera

Family Pteropodidae
Rousettus madagascariensis (N = 5)
  Acari: Parasitiformes
    Spinturnicidae (5)
  Acari: Acariformes
    Myobiidae (2)
    Sarcoptidae
      Chirobia (3)
      Teinocoptes (3)
    Chirodiscidae (3)
  Insecta: Diptera
    Nycteribiidae (3)

Family Vespertilionidae

Miniopterus fraterculus (N = 1)
  Acari: Parasitiformes
    Spinturnicidae
    Macronyssidae
  Acari: Acariformes
    Chirodiscidae

Myotis goudoti (N = 1)
  Acari: Parasitiformes
    Spinturnicidae
    Macronyssidae
  Acari: Acariformes
    Chirodiscidae

Order Rodentia

Family Muridae
Eliurus tanala (N = 3)
  Acari: Parasitiformes
    Laelapidae (3)
  Acari: Acariformes
    Trombiculidae (3)
    Glycyphagidae (1)
    Atopomelidae
      Listrophoroides (*Eulistrophoroides*) (2)
      Listrophoroides (*Pallistrophoroides*) (3)
  Insecta: Phthriraptera: Anoplura
    Unidentified family (1)

Eliurus majori (N = 7)
  Acari: Parasitiformes
    Ixodidae (1)
    Laelapidae (7)
  Acari: Acariformes
    Trombiculidae (6)

Atopomelidae
  Listrophoroides (Pallistrophoroides) (2)
Insecta: Phthiraptera: Anoplura
  Unidentified family (7)

Eliurus minor (N = 3)
  Acari: Parasitiformes
    Ixodidae (1)
  Acari: Acariformes
    Trombiculidae (3)
    Ereynetidae (1)
    Glycyphagidae (2)
    Atopomelidae
      Listrophoroides (Pallistrophoroides) (3)
  Insecta: Phthiraptera: Anoplura
    Unidentified family (1)

Eliurus webbi (N = 2)
Acari: Parasitiformes
    Laelapidae (1)
  Acari: Acariformes
    Trombiculidae (2)
    Atopomelidae
      Listrophoroides (Eulistrophoroides) (1)
      Listrophoroides (Pallistrophoroides) (2)
  Insecta: Phthiraptera: Anoplura
    Unidentified family (1)

Eliurus grandidieri (N = 11)
  Acari: Parasitiformes
    Ixodidae (1)
    Laelapidae (10)
    Pachylaelapidae (1)
  Acari: Acariformes
    Trombiculidae (11)
    Atopomelidae
      Listrophoroides (Eulistrophoroides) (8)
      Listrophoroides (Pallistrophoroides) (9)
  Insecta: Phthiraptera: Anoplura
    Unidentified family (1)

Gymnuromys roberti (N = 1)
  Acari: Parasitiformes
    Ixodidae
    Laelapidae
  Acari: Acariformes
    Trombiculidae
    Atopomelidae
      Listrophoroides (Pallistrophoroides)

Voalavo gymnocaudus (1)
  Acari: Parasitiformes
    Laelapidae
  Acari: Acariformes
    Trombiculidae

Atopomelidae
  Listrophoroides (Pallistrophoroides)
Insecta: Phthiraptera: Anoplura
  Unidentified family

Nesomys rufus (N = 6)
  Acari: Parasitiformes
    Ixodidae (3)
    Laelapidae (4)
    Pachylaelapidae (2)
  Acari: Acariformes
    Trombiculidae (6)
    Atopomelidae
      Listrophoroides (Pallistrophoroides) (6)
  Insecta: Phthiraptera: Anoplura
    Unidentified family (5)
  Insecta: Coleoptera
    Unidentified family (2)

Rattus rattus (N = 11)
  Acari: Parasitiformes
    Ixodidae (5)
    Laelapidae
      Laelaps nuttalli (Hirst, 1915) (2)
      Echinolaelaps echidninus (Berlese, 1887)
(1)
  Acari: Acariformes
    Trombiculidae (10)
    Glycyphagidae (3)
    Listrophoridae
      Afrolistrophorus (3)
    Gastronyssidae
      Yunkeracarus (1)
  Insecta: Phthiraptera: Anoplura
    Polyplacidae
      Polyplax spinulosa (Burmeister, 1839) (7)
  Insecta: Siphonaptera
    Unidentified family (1)

Class Aves

Order Coraciiformes

Family Brachypteraciidae

Atelornis crossleyi (N = 1)
  Acari: Acariformes
    Trombiculidae
    Pterolichidae
    Xolalgidae

Order Falconiformes

Family Accipitridae

Accipiter francesii (N = 1)
    Acari: Acariformes
        Syringophilidae
        Harpyrhynchidae
        Hypoderatidae
        Gabuciniidae
    Insecta: Phthiraptera: Mallophaga
        Unidentified family

Order Passeriformes

Family Philepittidae

Neodrepanis coruscans (N = 2)
    Acari: Acariformes
        Proctophyllodidae (1)
        Trouessartiidae (2)

Neodrepanis hypoxantha (N = 2)
    Acari: Parasitiformes
        Rhinonyssidae (1)
    Acari: Acariformes
        Proctophyllodidae (2)
        Trouessartiidae (2)

Philepitta castanea (5)
    Acari: Acariformes
        Syringophilidae (1)
        Proctophyllodidae
            Philepittalges rotundus (Atyeo, 1966) (5)
        Trouessartiidae
            Arthrogynalges (5)
    Insecta: Phthiraptera: Mallophaga
        Unidentified family (5)

Family Sylviidae

Nesillas typica (N = 2)
    Acari: Parasitiformes
        Rhinonyssidae (1)
    Acari: Acariformes
        Avenzoariidae (2)
        Trouessartiidae (2)
    Insecta: Phthiraptera: Mallophaga
        Unidentified family

Family Ploceidae

Foudia omissa (N = 2)
    Acari: Parasitiformes
        Ixodidae (1)
    Acari: Acariformes
        Trombiculidae (1)
        Proctophyllodidae (2)
        Avenzoariidae (2)
        Trouessartiidae (2)
        Xolalgidae (1)
    Insecta: Phthiraptera: Mallophaga
        Unidentified family (1)

Discussion

Comparison of the parasite fauna (compound parasite communities) of the RS d'Anjanaharibe-Sud with that of the RNI d'Andringritra (OConnor, 1996) reveals a strong similarity at the ordinal, familial, and generic levels. Because the collections examined from the RS d'Anjanaharibe-Sud included relatively few birds, no real comparisons between the sites can be made. The collection of mites of the family Hypoderatidae from *Accipiter francesii* marks the first record of this family from Madagascar.

Among the collections of mammals from the two sites, 21 host species were recorded in each survey, with 13 of the species common to both areas. In general, the composition of the parasite faunas of the major host groups sampled, tenrecid insectivores and nesomyine rodents, were similar in the two areas. Sample sizes for many of the species were too small to allow detailed comparison of the parasite faunas of those species. For example, eight specimens of *Microgale dobsoni* from the RS d'Anjanaharibe-Sud yielded seven parasite taxa, whereas the single specimen from the RNI d'Andringitra bore only one. Several new and interesting records can be noted, however. The collection of the genus *Notoedres* (Sarcoptidae) from *M. cowani* is the first report of this family from the Tenrecidae. The families Glycyphagidae and Rosensteiniidae are reported for the first time in association with *Setifer setosus*. The collections of Rosensteiniidae from this host are particularly interesting because this family has been previously reported only in association with bats and guano-inhabiting arthropods. The numerous specimens collected from five of the eight individual hosts examined strongly suggest a true as-

sociation rather than contamination, particularly since no specimens were recovered from any other host. The morphology of the mites is similar to that of guano-inhabiting Rosensteiniidae rather than showing the specializations of taxa that are true parasites of bats or arthropods. Future field studies should determine whether *S. setosus* commonly enter caves or other areas supporting bat populations.

Among rodent hosts, collections of the small atopomelid fur mites belonging to the subgenus *Listrophoroides* (*Eulistrophoroides*) were less common than in the collections from the RNI d'Andringitra. At that locality, these mites were present on four of four species of *Eliurus* and on *Nesomys rufus*, whereas at the RS d'Anjanaharibe-Sud, they were collected from only three of five species of *Eliurus* and not from *N. rufus*. Finally, the record of the genus *Yunkeracarus*, an intranasal parasite collected from *Rattus rattus*, marks the first collection of the family Gastronyssidae in Madagascar and the first collection of this genus from *R. rattus*. This genus is known from murid rodents in many parts of the world but, interestingly, has never been reported from the widespread commensal rats.

Acknowledgements

Literature Cited

OConnor, B. M. 1996. Parasitic and commensal arthropods of some birds and mammals of the Réserve Naturelle Intégrale d'Andringitra, Madagascar, pp. 136–141. *In* Goodman, S. M., ed., A floral and faunal inventory of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: With reference to elevational variation. Fieldiana: Zoology, n.s., **85:** 1–319.

Yunker, C. E. 1961. A sampling technique for intranasal chiggers (Trombiculidae). Journal of Parasitology, **47:** 720.

Chapter 7

Amphibians and Reptiles of the Anjanaharibe-Sud Massif, Madagascar: Elevational Distribution and Regional Endemicity

Christopher J. Raxworthy,[1] **Franco Andreone,**[2] **Ronald A. Nussbaum,**[3] **Nirhy Rabibisoa,**[4] **and Herilala Randriamahazo**[5]

Abstract

Before 1994 the Anjanaharibe-Sud Massif, including the Réserve Spéciale (RS) d'Anjanaharibe-Sud, had never been surveyed for amphibians and reptiles. During the rainy seasons of 1994 and 1996, surveys were made on the eastern and western slopes of the massif in moist and sclerophyllous montane forest between 800 and 2000 m elevation. Fifty-three species of amphibian and 40 species of reptile were recorded. Most of the species (89%) are restricted to rain forest, and five species appear to be endemic to the Anjanaharibe-Sud Massif. Although species diversity is similar on both the eastern and western slopes (at similar elevations), 30 species are restricted to a single slope only (between 1000 and 1700 m elevation), suggesting significant differences in community composition. Species diversity of both amphibians and reptiles declines with increasing elevation. A large component of the montane herpetofauna of the RS d'Anjanaharibe-Sud (above 1500 m elevation) also occurs on the massifs of Marojejy (74%) and Tsaratanana (74%). Considering all elevations, the herpetofauna of the RS d'Anjanaharibe-Sud is most similar to that of the Réserve Naturelle Intégrale (RNI) de Marojejy (64%). However, 22 species found in the RS d'Anjanaharibe-Sud that have widespread distributions in eastern Madagascar are not known in the RNI de Marojejy. Two barriers to dispersal are suggested between the Anjanaharibe-Sud and Marojejy massifs, the Androranga and Lokoho rivers. The rich species diversity, potential local endemicity, and unique biogeographic affinities to both the eastern and northern regions all demonstrate the importance of the RS d'Anjanaharibe-Sud within the protected area network of Madagascar.

Résumé

L'inventaire des amphibiens et des reptiles du massif d'Anjanaharibe-Sud, qui comprend la Réserve Spéciale (RS) d'Anjanaharibe-Sud, n'avait jamais été réalisé auparavant. Au cours de la saison des pluies des années 1994 et 1996, des inventaires ont été conduits sur les versants orientaux et occidentaux du massif, au sein de la forêt humide sempervirente de moyenne et de haute altitudes, entre 800 et 2000 m. Un total de 53 espèces d'amphibiens et de 40 espèces de reptiles a été répertorié. La majorité des espèces (89%) était restreinte à la forêt pluviale et

[1] CERC, Columbia University, 1200 Amsterdam Avenue, New York, NY 10027 U.S.A.
[2] Museo Regionale di Scienze Naturali, Via G. Giolitti, 36, 10123 Torino, Italy.
[3] Museum of Zoology, University of Michigan, Ann Arbor, MI 48109 U.S.A.
[4] Départment de Biologie Animale, Université d'Antananarivo, Antananarivo (101), Madagascar.
[5] Parc Botanique et Zoologique de Tsimbazaza, BP 4096, Antananarivo (101), Madagascar.

cing espèces semblent êntre endémiques du massif d'Anjanaharibe-Sud. Bien que la diversité spécifique soit équivalente entre les versants occidentaux et orientaux, à altitude équivalente, 30 espèces se rencontrent uniquement sur un seul versant, entre 1100 et 1700 m d'altitude, suggérant qu'il existe des différences importantes dans la composition des communautés d'amphibiens et de reptiles. La diversité spécifique des amphibiens et des reptiles diminue en fonction de l'augmentation de l'altitude. Une proportion importante de l'herpétofaune de la zone d'altitude de la RS d'Anjanaharibe-Sud (au-dessus de 1500 m) se rencontre également dans le massif du Marojejy (74%) et dans le massif du Tsaratanana (74%). En prenant en compte toutes les stations altitudinales inventoriées, la RS d'Anjanaharibe-Sud est similaire à la Réserve Naturelle Intégrale (RNI) de Marojejy (64%). Cependant, 22 espèces rencontrées dans la RS d'Anjanaharibe-Sud n'ont pas été inventoriées au sein de la RNI de Marojejy, alors qu'elles ont par ailleurs une distribution étendue au sein de la forêt pluviale de l'est de Madagascar. Les deux barrières naturelles à l'origine de la différence dans la distribution des espèces de reptiles et d'amphibiens pourraient être les rivières Androranga et Lokoho. La riche diversité spécifique, le potentiel d'endémisme local et les relations biogéographiques exceptionnelles vis à vis des régions du nord et de l'est de Madagascar démontrent l'importance de la RS d'Anjanaharibe-Sud dans le contexte du réseau d'aires protégées de Madagascar.

Introduction

The Anjanaharibe-Sud Massif in northern Madagascar (14°42'S, 49°26'E) is a north-south-oriented ridge about 20 km long with three summits between 1899 and 2064 m elevation. The primary vegetation of the massif is moist and sclerophyllous montane forest. Anjanaharibe-Sud is close to two major massifs in Madagascar, 45 km southwest of Marojejy, and 90 km southeast of Tsaratanana. The Anjanaharibe-Sud Massif does not have an extensive montane heathland (although the extreme summit above 1950 m does include a small area of heathland) and in this respect is unlike Marojejy and Tsaratanana, both of which have this vegetation type above 2000 m elevation. The 32,100 ha Réserve Spéciale (RS) d'Anjanaharibe-Sud, established in 1958, protects forest of the massif between 500 and 2064 m elevation (Nicoll & Langrand, 1989).

Before this study, no collections of amphibians and reptiles had been made in the Anjanaharibe-Sud region or reserve and the only published herpetological data consisted of a field observation of a single gecko species (Nicoll & Langrand, 1989). This contrasts with the nearby Réserve Naturelle Intégrale (RNI) de Marojejy, which was surveyed for amphibians and reptiles in the early 1970s (Guillaumet et al., 1975) and was subsequently surveyed by other herpetologists (Glaw & Vences, 1994; Raxworthy & Nussbaum, 1997).

During October and November 1994, as part of a multidisciplinary study, a herpetological survey was made of the highest summit and eastern side

of the RS d'Anjanaharibe-Sud at the start of the rainy season. This inventory was further enriched by a subsequent herpetological survey completed on the western side of the massif, which was made during January and February 1996, at the peak of the rainy season.

Study Sites

Field work was centered on six elevational transects, four on the eastern slope of the massif (in the Lokoho River basin), with the highest elevation transect also including the ridge, and two on the western slope (in the Antainambalana River basin).

Eastern Transects E1

E1—14°45.3'S, 49°30.3'E. Survey dates: 18–30 October 1994. Sampling days: 13. Altitude surveyed: 800–950 m. Habitat: primary to slightly disturbed moist montane forest.

E2—14°44.7'S, 49°27.7'E. Survey dates: 1–12 November 1994. Sampling days: 12. Altitude surveyed: 1100–1350 m. Habitat: primary moist montane forest.

E3—14°44.5'S, 49°26.5'E. Survey dates: 14–23 November 1994. Sampling days: 10. Altitude surveyed: 1500–1700 m. Habitat: primary moist montane forest.

Eastern and Ridge Transects

E4—14°44.8'S, 49°25.0'E. Survey dates: 24–28 November 1994. Sampling days: 5. Altitude surveyed: 1850–2000 m. Habitat: primary sclerophyllous montane forest mixed with areas dominated by bamboo and ericoid shrubs.

Western Transects

W1—14°46'S, 49°27'E. Survey dates: 25 January–3 February 1996. Sampling days: 10. Altitude surveyed: 1000–1100 m. Habitat: primary moist montane forest.

W2—14°46'S, 49°26'E. Survey dates: 5–11 February 1996. Sampling days: 7. Altitude surveyed: 1200–1600 m. Habitat: primary moist montane forest.

Materials and Methods

The four members of the herpetological field survey team were N. Rabibisoa (eastern survey), F. Andreone (western survey), H. Randriamahazo (western survey), and J. E. Randrianirina (western survey).

The surveys were done either during the start (October–November) or middle (January–February) of the rainy season, when species are breeding and activity is at its highest. Field techniques used to sample animals (by both day and night) were as follows: (1) pitfall trapping with drift fences, (2) visual and acoustic searching, and (3) refuge examination (under and in fallen logs and rotten tree stumps; under bark; under rocks; in leaf litter, root-mat, and soil; and in leaf axils of *Pandanus* screw palms and *Ravenala* traveler's palm).

The pitfall traps were buckets (275 mm deep, 290 mm top internal diameter, and 220 mm bottom internal diameter) with the handles removed and small holes (2 mm diameter) punched in the bottom to allow water drainage. Buckets were sunk into the ground along a drift fence made from plastic sheeting (0.5 m wide) stapled in a vertical position to thin wooden stakes, with the fence bottom sealed 50 mm deep into the ground using soil and leaf litter. The trap lines were checked each morning and late afternoon. After heavy rain, the traps were sponge-dried.

For the eastern transects, the drift fence (100 m in length) was positioned to run across the middle of each pitfall trap. Pitfall traps were positioned at both ends of the drift fence, with the other nine traps at 10 m intervals. Three lines were used, placed in the following forest types: ridge (along the crest of a ridge), slope (on a gradient, intermediate between ridge top and valley bottom), and valley (within 20 m of a stream in a valley bottom). This procedure was used on previous surveys (e.g., Raxworthy & Nussbaum, 1994, 1996b) and is recommended for use on future projects to allow standardization of capture techniques and subsequent comparisons of results.

For the western transects, pitfalls were placed adjacent to the drift fence, alternating on each side of the fence, and at each end, at 5 m intervals. Three lines 50 m long were used at the 1050 m transect, with 11 pitfalls per line. Two lines 60 m long were used at the 1400 m transect, with 13 pitfalls per line.

Visual searches and refuge examinations were made throughout the full elevation range of habitats available in the reserve. The majority of searching was done close to trails made during the study, although ridges and riverbanks were also used to orient search paths. Night searches were made using headlights.

The following information was recorded at the time of capture for each individual: date, time, longitude, latitude, altitude, microhabitat, and circumstances of capture. Animals not retained for specimens were returned to the site of original capture. Voucher specimens were fixed in 10% buffered formalin and later transferred to alcohol. Color slides were taken of representative live individuals of many species. Frog calls were recorded when possible. Collected material was deposited at four research collections: for the eastern survey, at the Département de Biologie Animale, Université d'Antananarivo, and the Museum of Zoology, University of Michigan; and for the western survey, at the Section de Zoologie, Parc Botanique et Zoologique de Tsimbazaza, Antananarivo, and the Museo Regionale di Scienze Naturali, Torino.

Results

Fifty-three amphibian and 40 reptile species were recorded at the RS d'Anjanaharibe-Sud (Table 7-1), including two subspecies and six amphibians and four reptiles that may represent new

Species	Transect*					
	E1 800– 950 m	E2 1100– 1350 m	E3 1500– 1700 m	E4 1850– 2000 m	W1 1000– 1100 m	W2 1200– 1600 m
AMPHIBIA						
MICROHYLIDAE						
Anodonthyla boulengeri				*	*	
Platypelis grandis	*	*			*	*
Platypelis cf. *occultans*					*	*
Platypelis pollicaris	*	*	*			
Platypelis tsaratananaensis			*	*		*
Platypelis tuberifera		*				*
Platypelis sp. 1		*	*			
Platypelis sp. 2		*				*
Platypelis sp. 3						*
Plethodontohyla laevipes		*				
Plethodontohyla minuta	*		*			
Plethodontohyla notosticta			*		*	*
Plethodontohyla serratopalpebrosa		*	*	*	*	*
Plethodontohyla sp. 1			*	*	*	
Plethodontohyla sp. 2	?	?	?	?		
Stumpffia grandis	*					
Stumpffia roseifemoralis	*	*	*			*
Stumpffia tetradactyla					*	*
RANIDAE						
Ptychadena mascareniensis	*					
MANTELLIDAE[+]						
Mantella sp. 1	*				*	
Mantidactylus aglavei	*	*			*	*
Mantidactylus albofrenatus	*	*	*		*	*
Mantidactylus asper		*			*	*
Mantidactylus betsileanus	*	*			*	
Mantidactylus bicalcaratus	*	*	*	*	*	*
Mantidactylus biporus	*	*				
Mantidactylus cornutus		*	*	*	*	*
Mantidactylus elegans				*		
Mantidactylus femoralis	*	*	*		*	
Mantidactylus flavobrunneus	*	*				
Mantidactylus grandidieri					*	
Mantidactylus grandisonae		*			*	*
Mantidactylus guttulatus		*				
Mantidactylus liber		*	*		*	
Mantidactylus luteus	*	*			*	
Mantidactylus opiparis		*			*	
Mantidactylus peraccae		*	*		*	*
Mantidactylus pulcher	*	*				*
Mantidactylus rivicola		*	*		*	
Mantidactylus redimitus	*				*	
Mantidactylus ulcerosus		*				
RHACOPHORIDAE[+]						
Aglyptodactylus madagascariensis				*	*	*
Boophis albilabris					*	
Boophis cf. *albipunctatus*		*				
Boophis cf. *brachychir*	*		*		*	*
Boophis erythrodactylus					*	
Boophis luteus cf. *septentrionalis*					*	
Boophis madagascariensis		*			*	
Boophis mandraka		*			*	
Boophis marojezensis		*	*		*	
Boophis rappiodes					*	
Boophis reticulatus	*	*	*		*	*
Boophis anjanaharibeensis					*	

TABLE 7-1. *Continued.*

Species	E1 800– 950 m	E2 1100– 1350 m	E3 1500– 1700 m	E4 1850– 2000 m	W1 1000– 1100 m	W2 1200– 1600 m
REPTILIA						
GEKKONIDAE						
Ebenavia inunguis	*					
Phelsuma guttata	*					
Phelsuma lineata	*	*				
Phelsuma quadriocellata	*	*				
Paroedura gracilis		*				*
Uroplatus cf. ebenaui		*			*	*
Uroplatus sikorae	*					
CHAMAELEONIDAE						
Brookesia betschi					*	*
Brookesia therezieni	*					*
Brookesia vadoni						*
Calumma brevicornis		*	*	*	*	*
Calumma gastrotaenia guillaumeti		*	*		*	*
Calumma gastrotaenia marojezensis	*					
Calumma malthe		*	*			
Calumma nasuta	*	*	*		*	*
Calumma parsoni		*			*	*
Furcifer pardalis	*					
SCINCIDAE						
Amphiglossus melanopleura			*			
Amphiglossus melanurus	*				*	*
Amphiglossus minutus	*	*			*	*
Amphiglossus mouroundavae						*
Amphiglossus punctatus		*				*
Amphiglossus cf. tsaratananaensis					*	*
Androngo crenni					*	
Mabuya gravenhorstii	*					
Paracontias hildebrandti					*	
CORDYLIDAE						
Zonosaurus madagascariensis	*	*			*	
BOIDAE						
Boa manditra	*	*				
TYPHLOPIDAE						
Typhlops mucronatus					*	
COLUBRIDAE						
Brygophis coulangesi						*
Geodipsas infralineata	*				*	
Geodipsas sp. 1			*	*		
Liophidium rhodogaster	*					*
Liophidium sp. 1	*					
Liophidium sp. 2	*					
Liopholidophis epistibes	*					
Liopholidophis infrasignatus						*
Lycodryas betsileanus	*					
Pseudoxyrhopus microps		*				
Pseudoxyrhopus tritaeniatus					*	
Pseudoxyrhopus sp. 1					*	
Total species	39	45	24	10	50	38

* E = eastern transects; W = western transects.

† The taxonomic rank of mantellines and rhacophorines is still uncertain. Most recently authors have considered them as either families (Blommers-Schlösser & Blanc, 1991) or subfamilies of Ranidae (Blommers-Schlösser, 1993; Glaw & Vences, 1994). Here we tentatively continue to give them the status of families.

taxa. In addition, another new species of amphibian, *Boophis anjanaharibeensis*, has now been described by Andreone (1996). A similar degree of species diversity (sometimes termed species richness; see Rosenzweig 1995:201, who recommends that this term be abandoned) was recorded on both sides of the massif: amphibian species, 44 east, 40 west; and reptile species, 29 east, 24 west. Species diversity was greatest at the lower elevation transects: 34 species of amphibians at transect W1 and 20 species of reptiles at transect E1. Species diversity was lowest at the highest transect (E4) for both amphibians (eight species) and reptiles (two species) (Table 7-1, Fig. 7-1).

The pitfall data are given in Tables 7-2 and 7-3. Eight amphibian and nine reptile species were captured in pitfall traps, among a sample of 30 individuals, during 1,458 trap-days. Overall pitfall capture success was 2% daily for amphibians and reptiles.

Discussion

Species Not Found

Nicoll and Langrand (1989) listed *Uroplatus fimbriatus* for the RS d'Anjanaharibe-Sud, a gecko we did not find during our surveys. It seems probable that this record is based on a personal observation without vouchers, because the most recent revision of *Uroplatus* (Bauer & Russell, 1989) does not list *Uroplatus* museum material for RS d'Anjanaharibe-Sud. We strongly suspect that this record of *U. fimbriatus* actually represents a misidentified *U. sikorae* (a species resurrected from synonymy with *U. fimbriatus* by Bauer & Russell, 1989), which we recorded at the lowest elevational transect (E1) on the eastern slopes of the RS d'Anjanaharibe-Sud.

Sampling

The herpetological capture success of the pitfall traps, 30 captures in 1,458 trap-days (2.1% daily trap success), is almost half that achieved by pitfall traps at RNI d'Andringitra, where 32 herpetological captures were made in 902 trap-days (3.5% daily trap success) (Raxworthy & Nussbaum, 1996b).

At the RS d'Anjanaharibe-Sud, pitfall capture success was especially poor for the eastern tran-
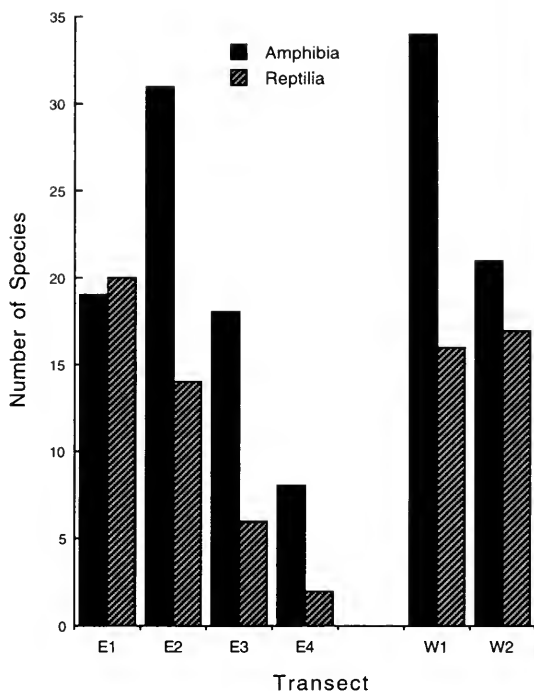
Fig. 7-1. Herpetofaunal diversity in each transect zone within the RS d'Anjanaharibe-Sud.

sects; just 13 individuals were caught in 1,045 trap-days (1.2% daily trap success) using a trapping method identical to that used at RNI d'Andringitra. It is not clear whether species susceptible to pitfall trapping are less abundant at the RS d'Anjanaharibe-Sud or whether lower trap rates might reflect seasonal differences in activity (pitfall trapping at the RNI d'Andringitra started 29 days later than at RS d'Anjanaharibe-Sud).

For the western transects, pitfall success was much higher: 17 individuals in 413 trap-days (4.1% daily trap success). However, these results are not directly comparable with those from RNI d'Andringitra because different pitfall sampling methods were used.

By the end of each transect sampling period, few species not previously recorded in the zone were being discovered for the eastern transects (Fig. 7-2), with the last day of surveying producing only 0–2 additional species per transect.

For the eastern transects, based on the species-accumulation curves, the best surveyed transects are E1 (800–950 m) and E3 (1500–1700 m), where just one additional species was found over the last 3 days of surveying. However, the sampling periods of 12 days at E2 (1100–1350 m)

TABLE 7-2. Characteristics and herpetological capture results for all pitfall lines.

Character	East Lines												West Lines				
	1	2	3	4	5	6	7	8	9	10	11	12	1	2	3	4	5
Descriptive																	
Altitude, m	890	850	850	1250	1230	1240	1550	1510	1500	1970	1930	1950	1060	1060	1060	1370	1440
Forest type*	R	V	S	R	V	S	R	V	S	R	V	S	V	S	R	S	S
Dates (day/month)																	
Start	19/10	19/10	20/10	4/11	4/11	4/11	15/11	15/11	15/11	24/11	24/11	24/11	29/1	29/1	29/1	6/2	6/2
End	28/10	28/10	28/10	10/11	10/11	10/11	21/11	21/11	21/11	30/11	30/11	30/11	3/2	3/2	3/2	12/2	12/2
Total trap-days	110	110	99	88	88	88	88	77	77	77	77	77	77	77	77	91	91
Results																	
Total captures	0	5	0	1	—	3	—	0	0	—	—	0	7	3	1	5	1
Total species	0	4	0	1	—	1	—	0	0	—	—	0	3	3	1	5	1
Daily capture success, %	0	5	0	1	—	3	—	0	0	—	—	0	9	4	1	5	1

* R = ridge; S = slope; V = valley.

and 5 days at E4 (1850–2000 m) were probably too short for a single researcher to make a complete survey, as five and three species, respectively, were found over the last 2 days of sampling.

For the western transects, three researchers worked over a 7- to 10-day period, compared with a single collector at the eastern transects. The greater collecting intensity in the western transects is reflected by the much greater rate of species acquisition during the first 2 days at each transect. By the final 2 days of surveying, only two additional species were sampled at W2 (1200–1600 m), but a diversity plateau was not evident at W1 (1000–1100 m), suggesting that surveying time was too short.

Elevational Distribution

Only one species, *Mantidactylus bicalcaratus*, a *Pandanus* screw palm frog, is distributed across the entire elevational range of all six transects (890–1950 m). Six amphibian species are found between E1 and E3 (950–1500 m), and three species are found between E2 and E4 (1350–1850 m). The reptiles appear to be more restricted in their elevational tolerance, with just two species occurring in three adjoining eastern transect zones. Both are chameleons: *Calumma brevicornis* (1300–1950 m) and *C. nasuta* (875–1580 m).

Despite the significant turnover in species with elevation in the RS d'Anjanaharibe-Sud, only two vegetation types are recognized within the survey transects: moist montane forest, typically between 800 and 1300 m, and sclerophyllous montane rain forest, typically between 1300 and 2000 m (White, 1983; Jenkins, 1987). The boundary between moist and sclerophyllous montane forest is actually difficult to determine because the two forest types intergrade (Raxworthy & Nussbaum, 1996a); in the RS d'Anjanaharibe-Sud, trees with sclerophyllous leaves were recorded only at the highest-elevation transect, 1850–2000 m. Surprisingly, herpetofaunal endemism is extremely low in this habitat, with only one species, *Mantidactylus elegans*, restricted to sclerophyllous forest on the Anjanaharibe-Sud Massif. This compares to 18 species (7 amphibians and 11 reptiles) restricted to moist montane forest below 1100 m elevation (rain forest endemics distributed in E1 and W1 only). The turnover of amphibians and reptiles in moist montane forest in the RS d'Anjanaharibe-Sud suggests that this single habitat type actually has several herpetological com-

TABLE 7-3. Herpetological capture results for all pitfall lines.

Species	East Lines												West Lines					Total Captures
	1	2	3	4	5	6	7	8	9	10	11	12	1	2	3	4	5	
AMPHIBIA																		
Platypelis grandis		1																1
Plethodontohyla notosticta																	1	1
Plethodontohyla serratopalpebrosa											1			1				2
Plethodontohyla sp. 1.											1							1
Stumpffia roseifemoralis		1																1
Mantidactylus asper													1					1
Mantidactylus opiparis														1				1
Mantidactylus redimitus		1																1
REPTILIA																		
Amphiglossus melanopleura							1											1
Amphiglossus melanurus																1		1
Amphiglossus minutus		1											5			1		7
Amphiglossus mouroundavae																1		1
Amphiglossus punctatus				1	1	3										1		6
Amphiglossus cf. *tsaratananaensis*															1	1		2
Androngo crenni														1				1
Liophidium rhodogaster		1																1
Pseudoxyrhopus sp. 1													1					1
Total	0	5	0	1	1	3	1	0	0	0	2	0	7	3	1	5	1	30
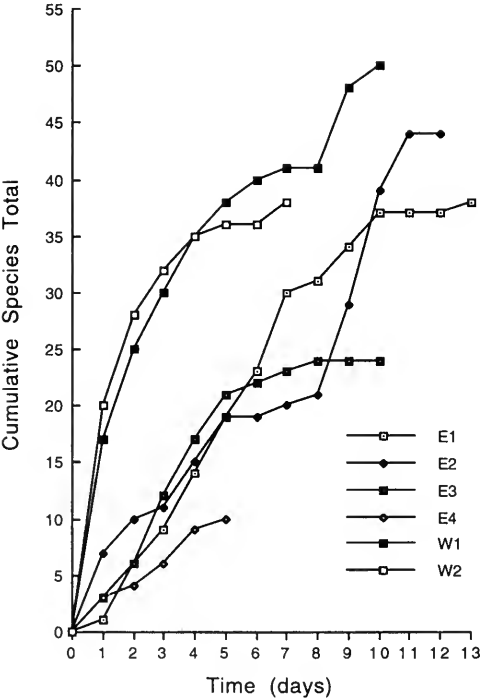
FIG. 7-2. Accumulation curves of herpetofaunal diversity (all sampling techniques) in each transect zone within the RS d'Anjanaharibe-Sud.

munities, each adapted to a narrower elevational range.

A 900 m transition in rain forest herpetofaunal communities was reported at Montagne d'Ambre (Raxworthy & Nussbaum, 1994). In the RS d'Anjanaharibe-Sud, this transition occurs between the E1 transect (800–950 m) and the higher elevation transects. A total of 12 species are restricted to below 950 m, 54 species are restricted to above 1000 m, and 26 species occur both above and below 950 m.

A summary of species diversity for each transect is shown in Figure 7-1. Amphibian species diversity declines above 1500 m elevation in the eastern transects and above 1200 m in the western transects. The amphibian species diversity for the lowest elevation transect, E1 (800–950 m), is lower than for the midelevation transect, E2, indicating a midelevation diversity bulge. For reptiles, there is an obvious negative relationship between elevation and species diversity in the eastern transects, but the two western transects have almost the same species diversity despite their different elevations.

These results are similar to elevational species diversity trends reported for the RNI d'Andringitra by Raxworthy and Nussbaum (1996b). On the Andringitra Massif, there is an obvious general decline in species diversity at

higher elevation, above the lowest elevation transect of 650–800 m for reptiles and above the second lowest elevation transect of 750–860 m for amphibians. Species diversity of both amphibians and reptiles is less than 10 species at transects above 1850 m elevation for both the Andringitra and Anjanaharibe-Sud Massifs.

There is no doubt that herpetofaunal species diversity decreases in montane regions of Madagascar (above 1500 m), but the factors responsible for this decline are unknown. A midelevation diversity bulge in species diversity was reported at the RNI d'Andringitra for amphibians (Raxworthy & Nussbaum, 1996b) and is also evident for amphibians on the Anjanaharibe-Sud Massif. Because trends in species diversity at low elevation (below 700 m) have not been described (largely because so little forest of this type still survives in Madagascar), it is not clear whether the midelevation diversity bulge also exists for reptiles. If this is the case, maximum reptile species diversity will occur at a lower elevation than that recorded for amphibians.

Elevational diversity gradients in general remain poorly understood, but tropical, midelevation diversity bulges have now been reported for bryophytes (Gradstein & Pocs, 1989), pteridophytes (Tryson, 1989), arthropods (Janzen et al., 1976), birds (Terborgh, 1977), and mammals (Heaney & Rickart, 1990). These patterns all appear to represent the unimodal productivity pattern of species diversity, which has been most recently reviewed by Rosenzweig (1995). Theories for the decrease phase (decreasing species diversity with higher productivity, such as at lower elevations) remain controversial, and none has yet gained widespread acceptance.

Eastern and Western Slopes

Table 7-1 shows obvious differences between the eastern and western transects of similar elevations. Comparisons made between the herpetofauna of transect E2 + E3 (1100–1700 m) and W1 + W2 (1000–1600 m) reveal 11 species found only on the eastern side and 19 species found only on the western side. Although these differences are large, interpretation of this result is complicated by the timing of the eastern and western surveys at different periods of the rainy season. Because changes in herpetofaunal species activity are typically not obvious between the start and middle of the rainy season (unlike the dramatic changes in activity that occur between the dry and rainy seasons), we consider it unlikely that survey timing could account for all sampling differences between the forests of the eastern and western flanks of the Anjanaharibe-Sud Massif.

Other possible explanations for these east-west differences concern the pitfall trapping methods used and the field collectors, which were not identical for the eastern and western forests surveys. If the pitfall trap data are removed from the analysis, this accounts for east-west differences in only four species: *Amphiglossus mouroundavae*, *Amphiglossus* cf. *tsaratananaensis*, *Androngo crenni*, and *Pseudoxyrhopus* sp. 1.

Although identical collecting methods were used, collecting ability inevitably varies among individuals. Incomplete surveying by collectors always produces a taxonomic bias toward those groups most frequently encountered and easy to capture. The species collected on the eastern and western transects do not indicate taxonomic bias toward easy-to-capture groups because cryptic groups such as microhylids (*Plethodontohyla*, *Platypelis*, and *Stumpffia*), chameleons (*Brookesia* and *Calumma*), and fossorial/semifossorial skinks (*Amphiglossus*) and snakes (*Pseudoxyrhopus*) are represented in both collections. Thus, differences in collecting ability among collectors are not obvious between the eastern and western transects.

Another potential sampling problem is that all of the transects appear not to have been surveyed for a sufficient period of time to ensure that all species were sampled (Fig. 7-2).

Although there may have been sampling biases that could account for some of the differences, we suspect that real differences exist between the herpetofaunal communities on the eastern and western flanks of the Anjanaharibe-Sud Massif. The differences are too great to be explained by sampling bias alone.

East-west herpetofaunal difference may result from the north-south orientation of the massif and the effect this orientation has on local climate. For much of the year, trade winds blow across Madagascar from the east (Donque, 1972), creating rain shadows on the western slopes of some massifs. (The most striking rain shadow we have observed occurs on the western flank of the Anosy Mountains, where moist montane forest and arid spiny forest may be separated by as little as 3 km.) In addition, solar radiation is unlikely to be the same on the east- and west-facing slopes. Differences in precipitation and solar radiation will certainly have significant effects on the habitats

on the eastern and western slopes and therefore are also likely to result in different herpetofaunal communities.

Regional Endemicity

Endemism of amphibians and reptiles at RS d'Anjanaharibe-Sud is summarized in Table 7-4. Most (89%) of the species are endemic to rain forest habitats in Madagascar. Those species not endemic to rain forest (moist and sclerophyllous) appear to be tolerant of human disturbance and are able to survive in agricultural or urban environments. None of these species is a specialist of the arid habitats that occur in southern and western Madagascar.

Two sites in close proximity to Anjanaharibe-Sud Massif were selected for regional comparison: Tsaratanana, 14°26'S, 49°46'E (90 km northwest of Anjanaharibe-Sud), and Marojejy, 14°11'S, 48°57'S (45 km northeast of Anjanaharibe-Sud). The Tsaratanana and Marojejy massifs are especially appropriate for comparison because both are montane rain forest sites with the same habitats as Anjanaharibe-Sud. Both sites are included in reserves (described in detail by Nicoll & Langrand, 1989) and were surveyed for amphibians and reptiles between 1992 and 1993 as part of a major rain forest survey in Madagascar (see Raxworthy & Nussbaum, 1997). The surveyed Marojejy rain forest includes the same elevational range as Anjanaharibe-Sud. In the surveyed region at Tsaratanana, rain forest below 1500 m was either heavily degraded or reduced to small fragments. Therefore, primary forest of this elevation could not be adequately surveyed.

Table 7-4 lists the species found at Anjanaharibe-Sud Massif that also occur on the Tsaratanana and Marojejy massifs. The majority of Anjanaharibe-Sud species (64%) are also found at Marojejy, compared with Tsaratanana, where only 36% of the Anjanaharibe-Sud herpetofauna is distributed. As expected, there is a close similarity between the Marojejy and Anjanaharibe-Sud herpetofaunas.

The smaller fraction of Anjanaharibe-Sud species shared with Tsaratanana, however, is misleading. This reflects the absence of lower elevation forest (below 1500 m) at Tsaratanana. Thus, lower elevation Anjanaharibe-Sud species such as *Platypelis grandis*, *Plethodontohyla laevipes*, *Mantella* sp. 1, *Boophis madagascariensis*, *Paroedura gracilis*, and *Uroplatus sikorae*, which are

known both east and west of the Tsaratanana Massif (Raxworthy & Nussbaum, unpubl. data), probably would have been recorded at Tsaratanana if lower elevation forest still existed at the survey site. However, the absence of some species at Tsaratanana that have a broad elevational range at Anjanaharibe-Sud (*Anodonthyla boulengeri*, *Mantidactylus bicalcaratus*, and *Mantidactylus cornutus*) suggests real biogeographic differences in the faunas of each massif.

A biogeographic comparison restricted to just the Anjanaharibe-Sud species recorded above 1500 m (transects E3 and E4) includes 27 species: 21 amphibians and 6 reptiles, all 27 of which are known from either Tsaratanana or Marojejy. Of these 27 montane Anjanaharibe-Sud species, 20 species (74%) occur at Tsaratanana and 20 species (74%) occur at Marojejy. The montane herpetofauna of Anjanaharibe-Sud is, therefore, equally similar to what is found on both these other massifs, despite the proximity of Anjanaharibe-Sud to Marojejy.

Five species recorded at Anjanaharibe-Sud are currently unknown from any other site and therefore are considered here to be endemic to the massif (Table 7-4). It seems likely that some or all of these species have a genuinely small distribution confined to the Anjanaharibe-Sud Massif because they have not been found during herpetofaunal surveys by us or others at other sites in the region.

The elevational ranges of all five potential endemics fall between 800 and 1600 m; and none is a high-elevation specialist (restricted to above 1500 m, see Raxworthy & Nussbaum, 1996a). This is surprising, because the forest of Anjanaharibe-Sud Massif, below 1500 m, extends continuously northward via Betaolana to Marojejy and via Andramanalana to Tsaratanana. Surveys at Betaolana and Andramanalana would determine whether these presumed Anjanaharibe-Sud endemics are actually restricted to the massif. The only isolated forest type at Anjanaharibe-Sud is above 1500 m elevation, yet no massif endemics are restricted to this elevational range. The biogeographic conditions that might have encouraged lowland speciation in the Anjanaharibe-Sud region are currently unknown.

A total of 22 species are recorded from Anjanaharibe-Sud, all of which are neither local endemics nor were found at Tsaratanana or Marojejy. These species all have widespread distributions in eastern Madagascar and are restricted to rain forest at low and middle elevations. Their absence at Tsaratanana is readily explained by the

TABLE 7-4. Distribution and endemicity of the Anjanaharibe-Sud Massif herpetofauna.

Species	Distribution		Endemicity	
	Tsaratanana 1500–2876 m	Marojejy 150–2133 m	Anjanaharibe-Sud Massif	Rain forest habitat
AMPHIBIA				
MICROHYLIDAE				
Anodonthyla boulengeri		*		*
Platypelis grandis		*		*
Platypelis cf. *occultans*				*
Platypelis pollicaris	*	*		*
Platypelis tsaratananaensis	*			*
Platypelis tuberifera		*		*
Platypelis sp. 1	*			*
Platypelis sp. 2				*
Platypelis sp. 3			*	*
Plethodontohyla laevipes				*
Plethodontohyla minuta	*	*		*
Plethodontohyla notosticta	*	*		*
Plethodontohyla serratopalpebrosa	*	*		*
Plethodontohyla sp. 1	*			*
Plethodontohyla sp. 2			*	*
Stumpffia grandis		*		*
Stumpffia roseifemoralis		*		*
Stumpffia tetradactyla				*
RANIDAE				
Ptychadena mascareniensis	*	*		
MANTELLIDAE				
Mantella sp. 1		*		*
Mantidactylus aglavei		*		*
Mantidactylus albofrenatus	*	*		*
Mantidactylus asper	*	*		*
Mantidactylus betsileanus				
Mantidactylus bicalcaratus		*		*
Mantidactylus biporus		*		*
Mantidactylus cornutus		*		*
Mantidactylus elegans	*†			*
Mantidactylus femoralis	*	*		*
Mantidactylus flavobrunneus				*
Mantidactylus grandidieri	*	*		*
Mantidactylus grandisonae	*	*		*
Mantidactylus guttulatus	*	*		*
Mantidactylus liber	*	*		*
Mantidactylus luteus		*		*
Mantidactylus opiparis	*	*		*
Mantidactylus peraccae	*	*		*
Mantidactylus pulcher		*		*
Mantidactylus rivicola		*		*
Mantidactylus redimitus		*		*
Mantidactylus ulcerosus				
RHACOPHORIDAE				
Aglyptodactylus madagascariensis	*	*		*
Boophis albilabris				*
Boophis cf. *albipunctatus*				*
Boophis cf. *brachychir*	*	*		*
Boophis erythrodactylus				*
Boophis luteus cf. *septentrionalis*	*	*		*
Boophis madagascariensis		*		*
Boophis mandraka	*			*
Boophis marojezensis	*	*		*
Boophis rappiodes			*	*

TABLE 7-4. *Continued.*

Species	Distribution		Endemicity	
	Tsaratanana 1500–2876 m	Marojejy 150–2133 m	Anjanaharibe-Sud Massif	Rain forest habitat
Boophis reticulatus	*	*	*	
Boophis anjanaharibeensis			*	
REPTILIA				
GEKKONIDAE				
Ebenavia inunguis		*		
Phelsuma guttata		*		*
Phelsuma lineata		*		
Phelsuma quadriocellata		*		*
Paroedura gracilis		*		*
Uroplatus cf. *ebenaui*	*	*		
Uroplatus sikorae		*		*
CHAMAELEONIDAE				
Brookesia betschi		*		*
Brookesia therezieni				*
Brookesia vadoni				*
Calumma brevicornis	*			*
Calumma gastrotaenia guillaumeti	*	*		*
Calumma gastrotaenia marojezensis		*		*
Calumma malthe	*	*		*
Calumma nasuta		*		
Calumma parsoni				*
Furcifer pardalis		*		
SCINCIDAE				
Amphiglossus melanopleura	*	*		*
Amphiglossus melanurus				*
Amphiglossus minutus				*
Amphiglossus mouroundavae		*		*
Amphiglossus punctatus		*		*
Amphiglossus cf. *tsaratananaensis*	*			*
Androngo crenni				*
Mabuya gravenhorstii	*	*		
Paracontias hildebrandti		*		*
CORDYLIDAE				
Zonosaurus madagascariensis	*	*		
BOIDAE				
Boa manditra		*		
TYPHLOPIDAE				
Typhlops mucronatus		*		*
COLUBRIDAE				
Brygophis coulangesi				*
Geodipsas infralineata		*		*
Geodipsas sp. 1	*			*
Liophidium rhodogaster		*		*
Liophidium sp. 1			*	*
Liophidium sp. 2				*
Liopholidophis epistibes		*		*
Liopholidophis infrasignatus				*
Lycodryas betsileanus		*		*
Pseudoxyrhopus microps		*		*
Pseudoxyrhopus tritaeniatus				*
Pseudoxyrhopus sp. 1			*	*
Total	33	60	5	83

[+] Data from Blommers-Schlösser and Blanc (1991).

lack of forest below 1500 m; the absence of such a large number of species at Marojejy, however, suggests barriers to dispersal.

Two barriers may have limited dispersal between Anjanaharibe-Sud and Marojejy, the Androranga and Lokoho rivers (including the Andapa basin) to the north and south of the Marojejy Massif, respectively. The only rain forest dispersal corridor that avoids these major rivers is the narrow Betaolana Ridge to the west of Marojejy, which is only 10 km wide in places. The Betaolana Ridge and the Androranga and Lokoho rivers may have acted as a filter, preventing some herpetofaunal species from dispersing into Marojejy. This may also explain the northern distribution pattern of other species, such as the lemur *Indri indri*, which occurs at Anjanaharibe-Sud but is absent at Marojejy. The narrow Betaolana Ridge dispersal corridor may also have isolated the Marojejy Massif sufficiently to account for the evolution of Marojejy endemics.

Conservation

The most vulnerable components of the RS d'Anjanaharibe-Sud herpetofauna are the apparently endemic species restricted to this massif. If their habitats at Anjanaharibe-Sud are destroyed, they may go extinct. The habitat requirements for all five endemic species (and 89% of the massif's herpetofauna) are primary montane forest. Therefore, effective conservation management of the massif depends completely on maintaining primary forest.

Our survey results suggest that faunal differences may exist between the eastern and western sides of the massif. It seems prudent, therefore, to balance conservation efforts so that both flanks of the massif receive equal degrees of protection and management intensity and, if necessary, to include more western forest within the reserve boundary.

The trends in deforestation occurring in and around the RS d'Anjanaharibe-Sud suggest that the lower elevation forest is under the greatest pressure for conversion to agricultural land. The forest below 1100 m elevation shows the greatest signs of degradation and is typically at the periphery of the surviving forest blocks. Our results for the Anjanaharibe Massif demonstrate that most species of amphibians and reptiles are restricted to a narrow elevational range and that the low-elevation forests include 25 species (27% of massif total) that are restricted to below 1100 m

elevation and 11 species (12% of massif total) that are restricted to below 950 m elevation (Table 7-1). If current levels of biodiversity are to be maintained, it is critical that peripheral lower elevation forest be protected. Because of the continuing loss of low-elevation forest, conservation efforts at the RS d'Anjanaharibe-Sud must concentrate on protecting this peripheral habitat rather than maintaining the core region of the reserve.

Acknowledgments

Literature Cited

ANDREONE, F. 1996. Another green treefrog *Boophis anjanaharibeensis* n.sp. (Ranidae: Rhacophorinae), from northeastern Madagascar. Aqua—Journal of Ichthyology and Aquatic Biology, 2:25-32.

BAUER, A. J., AND A. P. RUSSELL. 1989. A systematic review of the genus *Uroplatus* (Reptilia: Gekkonidae), with comments on its biology. Journal of Natural History, **23**: 169–203.

BLOMMERS-SCHLÖSSER, R.M.A. 1993. Systematic relationships of the Mantellinae Laurent 1946 (Anura Ranoidea). Ethology, Ecology and Evolution, **5**: 199–218.

BLOMMERS-SCHLÖSSER, R. M. A., AND C. P. BLANC. 1991. Amphibiens (première partie). Faune de Madagascar, **75**(1): 1–385.

DONQUE, G. 1972. The climatology of Madagascar, pp. 87–144. *In* Battistini, R., and G. Richard-Vindard,

eds., Biogeography and Ecology in Madagascar. Junk, The Hague, 765 pp.

GLAW, F., AND M. VENCES. 1994. A field guide to the amphibians and reptiles of Madagascar, 2nd edition. Moss Druck, Leverkusen, Germany, 480 pp.

GRADSTEIN, S. R., AND T. POCS. 1989. Bryophytes, pp. 311–325. In Leith, H., and M. J. R. Werger, eds., Ecosystems of the World, Vol. 14B. Tropical Rain Forest Ecosystems; Biogeographical and Ecological Studies. Elsevier Scientific, Amsterdam.

GUILLAUMET, J.-L., J.-M. BETSCH, C. BLANC, P. MORAT, AND A. PEYRIERAS. 1975. Etude des écosystémes montagnards dans la région malgache. III. Le Marojezy. IV. L'Itremo et l'Ibity. Géomorphologie, climatologie, faune et flore (Campagne RCP 225, 1972–1973). Bulletin de Muséum National d'Histoire Naturelle, 3rd Series, 309(Écologie Générale 25): 29–67.

HEANEY, L. R., AND E. A. RICKART. 1990. Correlations of clades and clines: Geographic, elevational, and phylogenetic distribution patterns among Philippine mammals, pp. 321–332. In Peters, G., and R. Hutterer, eds., Vertebrates in the Tropics. Museum Alexander Koenig, Bonn.

JANZEN, D. H., D. M. ATAROFF, M. FARINAS, S. REVES, N. RINCON, A. SOLER, P. SORIANO, AND M. VERA. 1976. Changes in the arthropod community along an elevational transect in the Venezuelan Andes. Biotropica, 8: 193–203.

JENKINS, M. 1987. Madagascar, an environmental profile. International Union for Conservation of Nature and Natural Resources, Cambridge, 374 pp.

NICOLL, M. E., AND O. LANGRAND. 1989. Madagascar: Revue de la Conservation et des Aires Protégées. World Wide Fund for Nature–Fonds Mondial pour la Nature, Gland, 374 pp.

RAXWORTHY, C. J., AND R. A. NUSSBAUM, 1994. A rainforest survey of amphibians, reptiles and small mammals at Montagne d'Ambre, Madagascar. Biological Conservation, 69: 65–73.

RAXWORTHY, C. J., AND R. A. NUSSBAUM. 1996a. Montane amphibian and reptile communities in Madagascar. Conservation Biology, 10: 750–756.

RAXWORTHY, C. J., AND R. A. NUSSBAUM. 1996b. Amphibians and reptiles of the Réserve Naturelle Intégrale d'Andringitra: A study of elevational distribution and local endemicity, pp. 158–170. In Goodman, S. M., ed., A floral and faunal inventory of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: With reference to elevational variation. Fieldiana: Zoology, New Series, 85: 1–319.

RAXWORTHY, C. J., AND R. A. NUSSBAUM. 1997. Biogeographic patterns of reptiles in eastern Madagascar, pp. 124–141. In Goodman, S. M., and B. D. Patterson, eds., Natural Change and Human Impact in Madagascar. Smithsonian Institution Press, Washington, D.C.

ROSENZWEIG, M. L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge, 436 pp.

TERBORGH, J. 1977. Bird species diversity along on an Andean elevational gradient. Ecology, 58: 1007–1019.

TRYSON, R. 1989. Pteridophytes, pp. 327–338. In Leith, H., and M. J. R. Werger, eds., Ecosystems of the World, Vol 14B. Tropical Rain Forest Ecosystems; Biogeographical and Ecological Studies. Elsevier Scientific, Amsterdam.

WHITE, F. 1983. The vegetation of Africa: A Descriptive Memoire to Accompany the UNESCO/AETFAT/UNSO Vegetation Map of Africa. Natural Resources Research 20. UNESCO, Paris, 356 pp.

Chapter 8

The Birds of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar

A. F. A. Hawkins,[1] Jean-Marc Thiollay,[2] and Steven M. Goodman[3]

Abstract

An elevational transect of the birds occurring in the Réserve Spéciale d'Anjanaharibe-Sud was conducted using a variety of techniques: point counts, general observations, and mist-netting. Ninety-four species were recorded in the reserve. The resident forest birds include 71 species at 875 m, 65 at 1260 m, 47 at 1550 m, and 22 at 1950 m.

Species-accumulation curves show that the majority of species (between 80% and 90%) recorded in each elevational zone were identified after 3 days of survey work. The optimum combination of methods that produced records of all the species recorded at all altitudinal samples was active searching and point counts.

Densities of more common species were assessed by point counts. Overall bird density was highest at 1250 m and 1550 m and significantly lower (by a factor of around 50%) at 875 m and 1950 m. Results suggest that the most efficient way to calculate species densities is to perform only one or two repeated samples at each point count site rather than the five used here.

Of 84 forest species, 60 were recorded frequently enough to show interpretable patterns of altitudinal distribution. Of these, 52 (86%) showed altitudinally limited distributions. At a crude level, the bird community can be divided into those that are more common below 1000–1200 m and those that are more common above this level. There was little evidence of morphologically or closely related and congeneric species replacing each other with altitude.

A study was conducted on the flocking behavior of forest species to test the hypothesis that predation pressure, or antipredator defense, may be the major factor of the grouping of foraging forest insectivores in mixed-species flocks.

Information is also presented on a comparison of mist-netting results between the elevational zones and general natural history information for selected species.

Résumé

Un inventaire des espèces d'oiseaux se rencontrant le long d'un transect altitudinal au sein de la Réserve Spéciale d'Anjanaharibe-Sud a été réalisé en utilisant plusieurs techniques; les points de comptage, les observations actives, et la capture au moyen de filets. Quatre vingt quatorze espèces ont été répertoriées au sein de la réserve. Les espèces forestières résidentes étaient au nombre de 71 à 875 m d'altitude, 65 à 1260 m, 47 à 1550 m, et 22 à 1950 m.

Les courbes cumulatives des espèces montrent qu'une majorité des espèces (entre 80 et 90%) relevées à chaque station altitudinale l'a été après 3 jours d'inventaire. La combinaison des

[1] BP 8511, Antananarivo (101), Madagascar.
[2] Laboratoire d'Ecologie, Ecole Normale Superieure, 46, rue d'Ulm, 75230 Cedex 05, France.
[3] Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, IL 60605-2496 U.S.A.

points de comptage et les observations aléatoires constitue la combinaison de méthodes optimale puisqu'elle a permis de déceler la présence de toutes les espèces aux différentes stations d'altitude.

Les densités des espèces les plus communes ont été déterminées à partir des points de comptage. Ces densités étaient les plus élevées à 1250 m et 1550 m et nettement inférieures, de l'ordre de 50%, à 875 et 1950 m d'altitude. Les résultats obtenus incitent à penser que la façon la plus efficace de calculer les densités des espèces est de réaliser un ou deux échantillonnages au niveau de chacun des points de comptage plutôt que d'en réaliser cinq comme habituellement.

Des 84 espèces forestières, 60 ont été répertoriées suffisamment de fois pour permettre la présentation de schémas de distribution altitudinale. Parmi elles, 52 (86%) présentent une limitation dans leur distribution altitudinale. Globalement, la communauté avienne peut être divisée en deux, les espèces communes au dessous de 1000–1200 m et celles qui sont communes au dessus de ce niveau d'altitude. Il y a peu d'évidence d'espèces proches sur les plans morphologiques, ou taxinomiques ou d'espèces placées dans un même genre, se remplaçant en fonction des niveaux d'altitude. Une étude a été réalisée sur la constitution de groupes plurispécifiques en milieu forestier afin de vérifier l'hypothèse que la pression de prédation engendrait la mise en place d'une stratégie anti-prédateur matérialisée par le regroupement de plusieurs individus appartenant à différentes espèces d'oiseaux forestiers insectivores.

Les informations relatives aux résultats de capture au moyen de filets réalisée aux différentes stations altitudinales sont aussi présentées, ainsi que des informations pertinentes sur l'histoire naturelle de certaines espèces sélectionnées.

Introduction

Over the past decade there has been a substantial increase in information on the birds of Madagascar, largely as a result of detailed biological inventories of poorly known forested areas. Several of these surveys have focused on elevational transects of mountainous areas, including the Parc National (PN) de la Montagne d'Ambre (Goodman et al., 1996), Réserve Naturelle Intégrale (RNI) de Zahamena (Hawkins et al., manuscript submitted), RNI de Marojejy (Safford & Duckworth, 1990), RNI d'Andringitra (Goodman & Putnam, 1996), and the RNI d'Andohahela (Goodman et al., 1997). As part of the biological inventory conducted on the Réserve Spéciale (RS) d'Anjanaharibe-Sud between 16 October and 2 December 1994, we conducted a survey of the birds occurring on the slopes of the reserve. The results are reported here.

Previous Work

The Mission Franco-Anglo-Américaine (FAA) spent the period from 19 August to 7 September 1930 "one day west of Andapa," on the upper limit of rain forest, apparently at about 1800 m, not far from the (now untraceable) village of Antanombo Manadriana (Rand, 1932, 1936). This site has been interpreted as lying about 30 km due west of Andapa, as this was the average daily distance covered by the FAA team (Carleton & Schmidt, 1990).

Rand (1936) describes forest near this site as being "in hilly country, . . . with moss and lichen-draped trees," with some "taller trees like those found at lower altitudes." Many species of bird were collected here, mostly by local hunters, although only 19 species are specifically mentioned for this site in Rand (1936). For the sake of this review, these records are treated as relating to the RS d'Anjanaharibe-Sud, although on the basis of data from other parts of Madagascar, including Langrand (1990), Safford and Duckworth (1990), and Goodman and Putnam (1996), it is unlikely that many of these species were collected at 1800 m. On the basis of Rand's (1936) notes on species at the site and examination of material collected during the mission, it is certain that information and specimens were collected from a wide variety of habitats, including wetlands, lowland forest, and montane humid forest. Thus, in reality, Rand's collectors must have ranged over a wider elevational range, and many specimens were taken at lower elevations.

Nicoll and Langrand (1989) presented a bird list from the RS d'Anjanaharibe-Sud, the result of visits made there in 1987 within the World Wide

Fund for Nature–Madagascar biodiversity and protected areas program. This list includes 42 species, 37 of which were not specifically mentioned in Rand (1936). All 42 species were recorded in the reserve during the 1994 inventory.

The period from 19 August to 26 October 1988 included visits to three sectors of the RNI de Marojejy, 40 km east of the RS d'Anjanaharibe-Sud, by the Cambridge Madagascar Rainforest Expedition (Safford & Duckworth, 1990). The RNI de Marojejy is linked to the RS d'Anjanaharibe-Sud by a narrow band of forest. Safford and Duckworth (1990) presented bird species lists for the RNI de Marojejy within the elevational range from 400 to 2137 m, permitting comparison with the results of the present study.

Systematic Order, Nomenclature, and Common Names

We generally follow the systematic order and English common and scientific names of Langrand (1990).

Goals

The principal purpose of the survey reported here was to detect as many of the bird species present in the reserve as possible. Within this general strategy, several more detailed questions were addressed:

1. What bird communities are present in each elevational zone, and at what densities do the common species occur?

2. How do bird species number, community composition, and overall abundance change with increasing elevation?

3. Is there evidence of replacement of morphologically or closely related and congeneric species with elevation in the bird community of the reserve?

4. Do bird species found at the same elevation occur at differing frequencies or densities in different microhabitats?

5. Is bird microhabitat selection within elevational zones related to overall elevational distribution?

6. Is predation pressure, or antipredator defense, a major cause of the grouping of foraging forest insectivores in mixed-species flocks?

7. What is the optimal survey period for avifaunal diversity assessment in eastern Malagasy humid forest?

8. What are the relative densities of understory birds as measured by mist-netting?

Methods

A full survey itinerary is presented in Chapter 1. In brief, between 16 October and 2 December 1994, 14 days were spent at 875 m, 14 days at 1250 m, 9 days at 1550 m, and 9 days at 1950 m. All observations were made within a zone of ±75 m in elevation and 2 km in horizontal distance from camps. An account of the vegetation and disturbance with each elevational zone is given in Chapter 2.

Active Searching

While an observer walked along forest paths, notes were made of birds seen or heard. Unfamiliar calls were investigated, and multispecies bird flocks were often followed until as many members as possible had been identified. A variant of this technique, static observation, was used from broken-canopy watch points, for raptors, aerial feeders, and canopy-feeding multispecies flocks.

In all elevational zones, Hawkins spent from 09:00 to about 12:00 and from 16:00 to 18:00 actively searching, after finishing point counts, and Goodman noted birds while checking small mammal traps, from 05:00 to 07:00 and from 15:00 to 17:00. At 875 and 1260 m, Thiollay spent from 05:30 to 17:00 actively searching. In addition, other team members provided incidental records.

Call Playback

Unfamiliar calls were recorded and then replayed to attract the calling bird to the vicinity of the observer. Additionally, prerecorded calls and songs of species considered likely to occur but difficult to detect were replayed along forest trails with the intent of provoking a response. Replay sites were separated by at least 150 m, and only one replay was made in each. Point-count sampling was conducted between 05:00 and 09:00, so

most call-playback samples were made between 09:00 and 10:00 and between 16:00 and 18:00.

Point Counts and Density Calculation

Assessments of bird species frequency and density were made by conducting point-count surveys (Reynolds et al., 1980; Bibby et al., 1992) within elevational zones. Point count sites were located along existing or newly cut trails within ±75 m elevation of the camp (referred to as the elevational zone) and were sampled by Hawkins between 05:00 (dawn) and 09:00. Newly cut trails were left for a 24 hr period before sampling. To maximize sample size by reducing intersite traveling time, samples were made in sequence along the trail. The intersample distance (125 m) was selected from prior experience with Malagasy forest birds and by reference to Recher (1981), Bibby et al. (1992), and Putnam and Goodman (in prep.). This distance was less than that over which some species were detectable, raising the possibility of duplicate contacts of loudly calling individuals. This possible confounding factor was minimized by noting all contacts detected from more than one sample site and eliminating those contacts subsequent to the first.

A minimum of 15 point-count sites were sampled within each elevational zone. Where possible, these sites were equally divided within each zone between ridges, slopes, and valley bottoms. At 1950 m, valleys were shallow and vegetation extremely dense. In this instance, seven point-count sites were established on ridges and eight in valleys. Simple vegetation structure measurements were made at each point-count site (Recher, 1981). They included estimates of canopy height and shrub and understory density. At each point-count site, four estimates of the distance visible through the vegetation (made at right angles to each other) were made at 1 m and 4 m height.

Each point-count site was counted five times, at least twice between 05:00 and 06:30 and at least twice between 06:30 and 09:00. Although a repeated sample gives less data than a new, independent sample, the limited elevational range of point-count sites and the difficulty of cutting trails reduced the potential for larger numbers of point-count sites. Comparison of species-accumulation curves was used to assess the optimal number of repeated samples from each point-count site.

During each sample count, which lasted for 10 min, the following data on each bird contact were

noted: species, estimated maximum distance from observer, nature of contact (song, call, wing noise, or visual), and time of contact. Wing noise was used only to estimate the distance at which a subsequently identified bird was first observed. Densities were calculated, using distance estimates, for those species for which sufficient data were collected. Sketch maps were drawn of the location of singing individuals of certain species as a control to permit comparisons with estimates of density made using point-count data and to prevent double counting of loudly calling species during point counts. Contacts clearly relating to mixed-species flocks were not used in density estimate calculations.

Densities were calculated using detection distances (grouped into intervals of 10 m below 100 m and 50 m between 100 and 200 m; distances over 200 m were not precisely estimated) using the computer program DISTANCE (Laake et al., 1993). Records of species on more than one repeated sample at the same site may have been related to the same individual. Such duplicate contacts were not used to calculate density (Buckland et al., 1993). It is probable that during any one visit to a point, some individuals of a species were not calling or otherwise detectable. Therefore, the maximum number of contacts with any one species during any one of the five repeated samples was used in the density calculations for that species. The use of the single maximum number of contacts for density calculation may, however, result in overestimation of the density of mobile species or those with home ranges larger than the distance (125 m) between point-count sites. This problem is discussed in more detail under "Problems with Density Calculations" (p. 111). If the maximum number of contacts in any one repeated sample was one, only the first contact distance was used.

DISTANCE (Laake et al., 1993) will calculate density estimates for any number of contacts, but 95% confidence intervals are large for samples of less than 15–20 contacts. Buckland et al. (1993) recommend a minimum of 60–100 contacts for a CV of about 20%.

Mist-netting

Mist nets were operated in each transect zone, in a variety of microhabitats (ridge, slope, and valley bottoms) and within 1 km ground distance of each camp. All nets used were 2.6 m high and

12 m long. A net left up for a 24-hour period is termed a "net-day." Nets were regularly checked during daylight hours, before dawn and after dusk, by M. Ravokatra and S. M. Goodman. In each zone, nine nets were run for 5 days, making a total of 45 net-days per transect, and were left up throughout the night to capture bats and nocturnal birds. The bottom panel of each net was generally within 10 cm of or touching the ground.

Most netted birds were marked for individual recognition and released. All birds caught on the same day had the same primary colored with indelible ink; e.g., birds caught on day 1 had the outermost primary on the left wing dyed. All birds were measured and weighed. Birds were released in the immediate vicinity of the net in which they were captured. Some birds were collected as voucher specimens or for taxonomic studies. These were prepared as either standard museum skins, fluid-preserved specimens, or full skeletons. Most of this material is housed in the Field Museum of Natural History, with a representative portion of the collection returned to the Département de Biologie Animale, Université d'Antananarivo. Tissue samples of collected specimens were saved in ethylenediaminetetraacetic acid (EDTA). Whole carcasses preserved in formalin were wrapped in fine cheesecloth before immersion to prevent mixing of ectoparasites (see Chapter 6). Blood smears were made of several released and collected birds for a study of blood parasites.

Bird Community Structure and Flocking Behavior

The underlying hypothesis of this study was that the greater the predation pressure on fully grown, independent birds by day, the greater their tendency to join moving flocks of birds when they had to forage. Actively foraging birds are more conspicuous than solitary foragers and potentially most at risk from predators because they are moving frequently, with reduced vigilance. The decrease in the number of specialized bird predators between the 875 and 1260 m zones (see Chapter 9) provided an opportunity to test whether there was a corresponding change in flocking patterns.

Between 05:30 and 17:00, birds were sought carefully by J. M. Thiollay, who walked slowly with frequent stops along footpaths within the two study areas used for raptors (see Chapter 9). Because of the limited number of trails, the same

TABLE 8-1. Survey effort and species numbers at each camp, with totals for the reserve.

Elevation (m)	No. of days	No. of point-count sites	No. of bird species recorded	No. of forest bird species recorded
875	14	20	74	71
1260	14	21	69	65
1550	9	15	49	47
1950	9	15	25	22
Total	46	71	94	84

paths were used up to six times during the study period (18 October–13 November) and often twice the same day.

All birds that were seen foraging within 20 m of the trail in natural forest understory were recorded, but not those along edges, in upper emergent trees, or in clearings. Flocks were followed outside the census strip only to determine their full composition. Each bird was categorized as being in a mixed flock (at least three individuals of two species within 10 m of each other and following the same path) or outside a flock (alone, in pairs, or with dependent fledglings). The proportion of birds encountered in each category was computed for each elevational zone separately. Besides the composition of each flock, the number of different flocks of any size encountered during each 1-hr period was recorded within the main daily period of birds' foraging activity (06:00–16:00, without rain). This gave a rough estimate of the frequency of flocks in each zone.

This method was intended to give to all species a similar probability of detection, independent of their vocal activity. This represented only a subset of the birds actually detected during the surveys because of restrictions of distance, behavior, and visibility, and it may not have been representative of the whole bird community. Birds most likely to be missed were those in low densities, and terrestrial, solitary, and secretive species, which rarely join mixed flocks.

Results

Bird Inventory

Table 8-1 shows survey effort for point counts in the four elevational zones. The number of hours spent actively searching was not quantified

TABLE 8-2. Species recorded in each elevational zone and elsewhere in the reserve (figures represent relative abundance at each elevational sample shown by the number of times the species was recorded on point counts).

Species	Guild†	Elevational zone				Seen elsewhere in reserve
		875 m	1260 m	1550 m	1950 m	
Lophotibis cristata‡	TIF	*	*	*		
Dendrocygna viduata	W					*
Aviceda madagascariensis‡	P	*	*	*		
Milvus migrans	P		*			
Eutriorchis astur‡	P	*				
Polyboroides radiatus‡	P	*	*			
Accipiter henstii‡	P	1			*	
Accipiter madagascariensis‡	P	*	*			
Accipiter francesii‡	P	*	*	*		
Buteo brachypterus‡	P	2	*	*	*	
Falco newtoni	P/I					*
Falco zoniventris‡	P/I	*	*			
Falco eleonorae§	P/I				*	
Mesitornis unicolor‡	TIF	*				
Dryolimnas cuvieri‡	TIF	*				
Canirallus kioloides‡	TIF	3	*	*		
Sarothrura insularis‡	TIF	1	3	2		
Streptopelia picturata‡	TF	4	6	5	*	
Treron australis‡	AF	*				
Alectroenas madagascariensis‡	AF	7	14	1		
Coracopsis vasa‡	AF	*	*			
Coracopsis nigra‡	AF	20	27	19	5	
Cuculus rochii‡	GI	32	32	10	1	
Coua serriana‡	TIF	20	*			
Coua reynaudii‡	TIF	10	7	6	3	
Coua caerulea‡	SGI	20	12	1	*	
Coua cristata‡	SGI					*
Centropus toulou‡	GI/F	18	1			
Otus rutilus‡	P/I	1	*	*		
Asio madagascariensis‡	P	*	*			
Caprimulgus madagascariensis‡	SI					*
Caprimulgus enarratus‡	SI	*				
Zoonavena grandidieri‡	SI	*	*	*	*	
Apus melba	SI	*	*		*	
Apus barbatus	SI	*	*	*	*	
Ispidina madagascariensis‡	SGI	1				
Merops superciliosus‡	SI	*				
Eurystomus glaucurus‡	SI	7	1	*		
Brachypteracias leptosomus‡	SGI	3	4			
Brachypteracias squamiger‡	TIF	3				
Atelornis pittoides‡	TIF		*			
Atelornis crossleyi‡	TIF		14	10	14	
Leptosomus discolor‡	SGI	12	9	*		
Philepitta castanea‡	AF	1	3	1		
Neodrepanis coruscans‡	ANI		27			
Neodrepanis hypoxantha‡	ANI			11	16	
Phedina borbonica‡	SI		*	*	*	
Motacilla flaviventris	TI			*		
Coracina cinerea‡	SGI	9	10	4		
Phyllastrephus madagascariensis‡	GI	12	4			
Phyllastrephus zosterops‡	GI	9	*			
Phyllastrephus cinereiceps‡	GI	*	4	4		
Hysipetes madagascariensis‡	AF	32	12	14	12	
Copsychus albospecularis‡	TI	10	14	*		
Saxicola torquata‡	TI			*	1	
Pseudocossyphus sharpei‡	TI	*	11	13	17	
Acrocephalus newtoni‡	GI					*
Nesillas typica‡	TI		24	30	35	
Cisticola cherina	TI					*
Dromaeocercus brunneus‡	TI	1	15	9	2	

TABLE 8-2. *Continued.*

| Species | Guild† | Elevational zone | | | | Seen elsewhere in reserve |
		875 m	1260 m	1550 m	1950 m	
Randia pseudozosterops‡	GI	*	2	*		
Cryptosylvicola randrianasoloi‡	GI	*	16	25	16	
Newtonia amphichroa‡	GI	1	20	13	13	
Newtonia brunneicauda‡	GI	27	24	18	7	
Newtonia fanovanae‡	GI					*
Neomixis tenella‡	GI	9	2			
Neomixis viridis‡	GI	21	14	6		
Neomixis striatigula‡	GI	21	20	3		
Hartertula flavoviridis‡	GI		*			
Pseudobias wardi‡	SI	1	7	2		
Terpsiphone mutata‡	SI	20	15	2		
Oxylabes madagascariensis‡	TI	4	7	2		
Crossleyia xanthophrys‡	TI		*	3		
Mystacornis crossleyi‡	TI	6	9			
Nectarinia souimanga‡	ANI	33	46	32	28	
Nectarinia notata‡	ANI	12	8	2		
Zosterops maderaspatana‡	GI/F	20	18	14	4	
Calicalicus madagascariensis‡	GI	24	13	*		
Schetba rufa‡	SGI	17				
Vanga curvirostris‡	SGI	2				
Leptopterus viridis‡	GI	5	11	1		
Leptopterus chabert‡	SI	4	1			
Cyanolanius madagascarinus‡	GI	13	10			
Oriolia bernieri‡	GI	*				*
Euryceros prevostii‡	SGI	5	1			
Hypositta corallirostris‡	GI	*	*			
Tylas eduardi‡	SGI	2	4	*		
Dicrurus forficatus‡	SI	15	14			
Corvus albus	O					*
Hartlaubius auratus‡	AF	*				
Ploceus nelicourvi‡	GI	2	5	2		
Foudia omissa‡	TF	6	1	12	5	
Foudia madagascariensis‡	TF	4	1	1		
Lonchura nana	TF	*	*			
Total species		74	69	49	25	
Total forest species		71	65	47	22	

* Present in survey area but not recorded on point counts.

† AF = arboreal frugivore; ANI = arboreal nectarivore/insectivore; GI = gleaning insectivore; GI/F = gleaning insectivore/frugivore (includes granivore); O = omnivore; P = predator; P/I = predator/insectivore; TF = terrestrial frugivore (includes granivore); TI = terrestrial insectivore; TIF = terrestrial insectivore/frugivore (includes granivore); SGI = sally-gleaning insectivore; SI = sallying insectivore; and W = aquatic. Guild memberships are taken from Langrand (1990), Eguchi et al. (1993), Hawkins (1994), and Goodman and Putman (1996).

‡ Considered to occur regularly within forest.

§ Boreal winter migrant.

but was proportional to the number of days spent at each altitudinal sample. Ninety-four species of bird were recorded in the reserve during the study (Table 8-2), of which 84 (89%) are species regularly found in forest (Langrand, 1990, 1995; Safford & Duckworth, 1990; pers. obs.). The only inventory method that revealed species not detected by any other method was active searching. Table 8-2 summarizes the elevational distribution of birds recorded in each zone (revealed by active searching) and their contact frequency on point counts.

CALL PLAYBACK—Table 8-3 shows location and frequency of prerecorded call-playback samples within each elevational zone. The only response detected to these call-playback attempts was one *Brachypteracias squamiger*, which responded at 09:20 in the 875 m elevational zone.

TABLE 8-3. Number of samples of prerecorded call-playback surveys.

Species	Elevational zone			
	875 m	1250 m	1550 m	1950 m
Mesitornis unicolor	13	12	6	0
Sarothrura watersi	0	4	3	5
Cuculus audeberti	12	8	6	0
Brachypteracias squamiger	8	0	0	0
Newtonia fanovanae	17	8	0	0

MIST-NETTING—Data on mist-net captures in each elevational zone are summarized in Table 8-4.

COMPLETENESS OF INVENTORY—Species-accumulation curves (Fig. 8-1) for each elevational zone indicate that the majority of species were located (by a combination of three survey techniques) during the first 3 days. Only at 1550 m were significant numbers of species found between the third and fifth days. At both 875 m and 1250 m species were added during the last 3 days. At 875 m these species included one not seen elsewhere in the reserve (*Eutriorchis astur*) and three seen commonly at higher elevations. At 1260 m species discovered late in the survey period included two large, scarce species (*Lophotibis cristata* and *Asio madagascariensis*) and two species of vanga (*Schetba rufa* and *Euryceros prevostii*) that may have wandered up from lower elevations during a period of exceptionally clear and sunny weather.

Several species recorded in other eastern Malagasy forest sites were not detected in the RS

TABLE 8-4. Results of mist-netting as presented by elevational transects in the RS d'Anjanaharibe-Sud.

Species	Elevational zone*				
	875 m (45)	1260 m (45)	1550 m (45)	1950 m (45)	Total (180)
Streptopelia picturata			2		2
Otus rutilus		2	2		4
Ispidina madagascariensis	1				1
Atelornis crossleyi			1	2	3
Philepitta castanea	1	3	9	0	13
Neodrepanis coruscans		5			5
Neodrepanis hypoxantha			9	6	15
Phyllastrephus madagascariensis	8				8
Phyllastrephus zosterops	8	1			9
Phyllastrephus cinereiceps		5	2		7
Hypsipetes madagascariensis	1		4	1	6
Copsychus albospecularis	7	3			10
Pseudocossyphus sharpei			3	2	5
Nesillas typica		6	15	11	32
Dromaeocercus brunneus				1	1
Newtonia amphichroa		5	6		11
Terpsiphone mutata	6	6			12
Oxylabes madagascariensis	2	1	4		7
Nectarinia souimanga	1	2	6	1	10
Nectarinia notata	1				1
Zosterops maderaspatana			2		2
Ploceus nelicourvi	2	2	3		7
Foudia madagascariensis	6				6
Foudia omissa	2	5	17	3	27
Total individuals	46	46	85	27	204
Total species	13	13	15	8	24
Average no. of birds captured per net-day	1.0	1.0	1.9	0.6	1.1

* Numbers in parentheses are the cumulative number of net-days within each elevational zone (see pp. 96–97 for definitions).
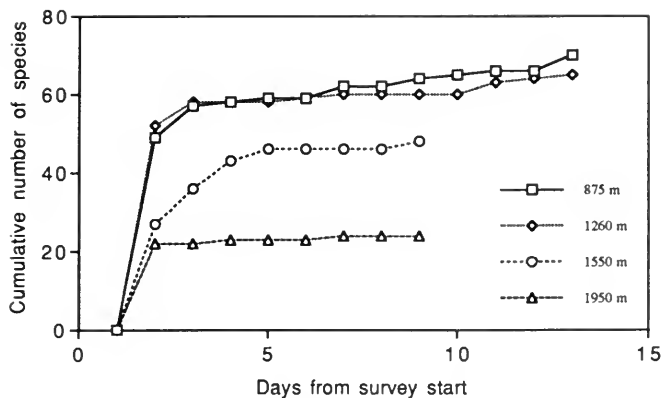
FIG. 8-1. Species accumulation curves for the four elevational zones. All bird inventory techniques combined.

d'Anjanaharibe-Sud during the survey. *Cuculus audeberti* is a rare resident or visitor to Madagascar known from a few specimens taken in eastern rain forest and two recent records (Langrand, 1990; Langrand & Sinclair, 1994; Goodman & Putnam, 1996). A single call heard at 875 m on 17 October was probably this species, but no similar calls were heard.

Tyto soumagnei is an apparently rare or at least difficult to locate forest owl, recently recorded from Antanamangotroka, not far from the RS d'Anjanaharibe-Sud (Halleux & Goodman, 1994; see also p. 121), PN de la Montagne d'Ambre (Goodman et al., 1996), Masoala Peninsula (Thorstrom & Watson, 1994), and Mantadia (Powzyk, 1995).

Ninox superciliaris was recorded several times in the nearby RNI de Marojejy in 1988 (Safford & Duckworth, 1990), in secondary forest, coffee plantations, and disturbed lowland forest between 500 and 900 m. In the present study, these habitats were either absent from study areas or not visited during evening periods, when detection of this species is most probable.

Phyllastrephus tenebrosus is known from only a few recent records, mostly from lowland forests, Masoala Peninsula and Baie d'Antongil (Langrand, 1990), RNI de Zahamena (Randriamanindry, 1995), RS d'Analamazaotra (Langrand, 1990), and PN de Ranomafana (Zack, pers. comm.). It was not recorded from the RNI de Marojejy during 3 months of field work in 1988 (Safford & Duckworth, 1990), or at RS d'Ambatovaky during 2 months of field work in 1989 (Thompson & Evans, 1991). Its known elevational range is 0–1000 m. It seems likely to be a lowland spe-

cialist present at low densities and difficult to observe.

Dromaeocercus seebohmi is known from fallow rice paddies and high-elevation heathland (Langrand, 1990; Goodman & Putnam, 1996). A short visit was made to a small area of mixed fallow rice paddy and marsh at 1000 m on 4 December, but no *Dromaeocercus* were seen.

Xenopirostris polleni appears to be more widespread in the southern half of the eastern Malagasy rain forest belt, being present at PN de Ranomafana (Zack pers. comm.), RNI d'Andringitra (Goodman & Putnam, 1996), and RNI d'Andohahela (Goodman et al., 1997). The only recent records from north of Ranomafana are from near Maroantsetra (Langrand, 1990), the RNI de Zahamena (Hawkins et al., manuscript submitted), and near Périnet (Langrand, 1995), although Benson et al. (1977) described a record that may have been this species from the RNI de Marojejy.

The following nonforest species were recorded by Rand (1936) in the general area of the RS d'Anjanaharibe-Sud but not on the 1994 mission: *Rallus madagascariensis*, *Sarothrura watersi*, *Margaroperdix madagascarensis*, and *Dromaeocercus seebohmi*.

Point Counts

Results from point-count samples were used to reveal variation in overall patterns of community characteristics with elevation, patterns of species distribution within elevational samples, according to the microhabitat variation, and to calculate densities of individual species. These were then re-

TABLE 8-5. Mean number of contacts and mean number of species per point-count site and overall bird density estimate within each sampling stratum (valley, slope, and ridge) in each elevational zone.*

Sampling stratum (no. of point-count sites)	Mean no. of contacts per sample (± SD)	Mean no. of species per sample over 5 repeated samples (± SD)	Overall bird density estimate (birds/km²) (95% CI)†
875 m			
Ridge (n = 6)	28.00 (±4.98)	22.00 (±2.68)	3,573 (2,380–5,363)
Slope (n = 7)	26.86 (±3.98)	20.86 (±3.76)	5,755 (3,642–9,092)
Valley (n = 7)	23.00 (±2.08)	18.29 (±0.76)	16,585 (7,768–35,409)
Overall	25.85 (±4.29)	20.30 (±3.01)	
1250 m			
Ridge (n = 7)	24.29 (±4.15)	18.28 (±4.42)	28,480 (10,062–80,608)
Slope (n = 7)	24.00 (±2.38)	20.86 (±1.34)	12,168 (8,344–17,742)
Valley (n = 7)	25.85 (±5.21)	22.29 (±4.11)	16,358 (11,140–24,608)
Overall	24.64 (±3.92)	20.62 (±3.72)	15,394 (12,091–19,600)
1550 m			
Ridge (n = 5)	18.00 (±4.06)	13.20 (±2.86)	23,647 (7,955–70,293)
Slope (n = 5)	19.00 (±3.74)	14.00 (±2.55)	28,330 (7,959–100,083)
Valley (n = 5)	18.00 (±3.11)	14.40 (±0.89)	6,299 (3,955–10,032)
Overall	18.33 (±3.04)	13.87 (±2.20)	12,751 (8,359–19,451)
1950 m			
Ridge (n = 7)	11.25 (±2.55)	8.50 (±1.77)	2,352 (1,562–3,541)
Valley (n = 8)	12.71 (±3.25)	9.43 (±2.57)	6,654 (4,172–10,611)
Overall	11.93 (±2.89)	8.93 (±2.15)	

* Overall bird density was not calculated for the 875 and 1950 m zones because density estimates for some sampling strata were significantly different. See p. 96 for discussion of significance levels.
† CI = confidence interval.

lated to vegetation structure variables measured at the point-count sites.

BIRD COMMUNITY CHARACTERISTICS—Table 8-5 shows variation in bird community parameters with elevation. Within elevational zones, the only significant differences between habitats are (1) that species number, contact frequency (Mann-Whitney U test), and density are all significantly lower in valley forest than in ridge forest at 875 m and (2) that density is significantly lower on ridge than in valley samples at 1950 m.

All pairwise comparisons of overall density, overall species number, and overall contact frequency between elevational zones are significant ($p < 0.05$, Mann-Whitney U test) except those between overall species numbers and contact fre-

quencies between the 875 m and 1250 m zones and density between the 1250 m and 1550 m zones.

MICROHABITAT VEGETATION STRUCTURE—Table 8-6 shows the variation of vegetation structure measures with sample location and elevation. The only significant differences of vegetation structure measures within elevational zones are that canopy height is significantly higher on slopes and in valleys than on ridges at 875 m and significantly higher in valleys than on either slopes or ridges at 1260 m. Shrub density is significantly greater at 1 m and 4 m on ridges than in valleys at 1950 m. All measures were tested with Kruskal-Wallis tests ($p > 0.05$ except for those cases noted above).

TABLE 8-6. Shrub density and canopy height variation with elevation and sample location.

| Elevation | Inverse shrub density* | | Canopy height (m) |
	1 m	4 m	
875 m			
Ridge (n = 6)	3.83 ± 1.03	9.36 ± 3.11	18.17 ± 1.83
Slope (n = 7)	6.30 ± 1.14	13.5 ± 3.75	30.00 ± 5.00
Valley (n = 7)	4.21 ± 2.55	10.56 ± 6.81	25.70 ± 9.39
1260 m			
Ridge (n = 7)	2.85 ± 1.57	7.71 ± 4.16	11.00 ± 3.36
Slope (n = 7)	3.68 ± 1.33	6.29 ± 1.55	9.85 ± 2.73
Valley (n = 7)	4.36 ± 1.89	11.11 ± 6.60	19.43 ± 4.19
1550 m			
Ridge (n = 5)	1.87 ± 0.75	5.96 ± 4.78	8.5 ± 3.27
Slope (n = 5)	3.21 ± 1.49	4.79 ± 1.24	12.67 ± 4.80
Valley (n = 5)	3.13 ± 0.53	7.38 ± 0.17	12.50 ± 3.53
1950 m			
Ridge (n = 7)	1.15 ± 0.22	2.10 ± 0.24	3.20 ± 0.45
Valley (n = 8)	2.50 ± 1.22	4.21 ± 1.12	5.29 ± 1.60

* Meters visible through vegetation. A lower number represents a higher relative shrub density.

Table 8-6 shows that there is an overall decrease in canopy height and an increase in shrub density with elevation. Within elevational zones there is a general tendency, most marked at lower elevations, for the canopy to be lower on ridges than in valleys and (more marked at higher elevations) for shrub layer densities to be higher on ridges.

SPECIES VARIATION WITH MICROHABITAT—Table 8-7 shows variations in contact frequencies on point counts between microhabitat samples within elevational zones. Few species of bird differed markedly in abundance between the three habitat types within any elevational zone. At 875 m, four species were more than twice as frequently recorded in one habitat type than any other: *Coua reynaudii* in ridge forest, *Schetba rufa* in slope forest, *Leptopterus chabert* in valley forest, and *Foudia omissa* in ridge forest.

At 1250 m, *Leptopterus viridis* and *Cyanolanius madagascarinus* were both recorded rarely in ridge forest compared with valley and slope forest, whereas *Dicrurus forficatus* and *Ploceus nelicourvi* showed the opposite tendency. At 1550 m, *Cuculus rochii* was recorded more than twice as often in ridge and slope forest as valley forest, *Atelornis crossleyi* was recorded less than half as frequently in ridge forest as slope forest, and *Neomixis viridis* was less regularly recorded in slope and ridge forest than valley forest. At 1950 m, *Coracopsis nigra* (ridge forest) and *Newtonia brunneicauda* (valley forest) were more than twice as common in one habitat than the other.

BIRD DENSITIES—Calculation of density using the DISTANCE program (Laake et al., 1993) requires a minimum of 15–20 contacts for meaningful density estimates. Within any one elevational zone, few species were recorded more than 15 times within one habitat type (ridge, valley, or slope). However, equally few species were recorded at greatly different frequencies within the different habitat types (Table 8-7). Therefore, densities within habitat types were not calculated; instead, overall densities within the elevational zone were calculated using data from all three habitat types for species recorded more than 15 times within an elevational zone (Table 8-8).

Coracopsis nigra, *Centropus toulou*, *Coua serriana*, and *Cuculus rochii* were detected more than 15 times on point counts at 875 and/or 1250 m but were omitted from this analysis because almost all contacts were at distances of more than 200 m. Density estimates calculated using such data had confidence intervals spanning two or more orders of magnitude.

Pooled density estimates were calculated for species with more than 10 contacts per elevational zone. Confidence intervals of density estimates are greatly improved by the increase in sample size produced by such pooling when there is no prior reason for considering densities different between samples (Buckland et al., 1993). Pooled estimates were calculated only from elevational zones in which contact frequency varied by less than 100%.

TABLE 8-7. Maximum number of contacts for each species detected at point-count sample sites within all elevational zones, by habitat type (ridge, slope, valley).

Elevational zone*

Species	875 m				1260 m				1550 m				1950 m			
	R	S	V	T	R	S	V	T	R	S	V	T	R	S	V	T
Accipiter henstii	0	1	0	1												
Buteo brachypterus	1	1	0	2												
Canirallus kioloides	0	0	3	3												
Sarothrura insularis	1	0	0	1												
Streptopelia picturata	3	1	0	4	2	0	1	3	2	0	0	2				
Alectroenas madagascariensis	2	2	3	7	3	1	2	6	0	2	3	5				
Coracopsis nigra	8	5	7	20	4	5	5	14	8	6	5	19	4		1	5
Cuculus rochii	10	10	12	32	11	7	9	27	5	4	1	10	1		0	1
Coua serriana	6	7	7	20												
Coua reynaudii	6	2	2	10	1	3	3	7	2	2	2	6	2		1	3
Coua caerulea	8	8	4	20	3	4	5	12	1	0	0	0				
Centropus toulou	7	5	6	18	1	0	0	1								
Otus rutilus	0	0	1	1												
Ispidina madagascariensis	0	1	0	1												
Eurystomus glaucurus	2	2	3	7	0	0	1	1								
Brachypteracias leptosomus	0	3	0	3	3	0	1	4								
Brachypteracias squamiger	0	1	2	3												
Atelornis crossleyi					6	4	4	14	2	5	3	10	6		8	14
Leptosomus discolor	5	4	3	12	4	3	2	9								
Philepitta castanea	0	0	1	1	1	0	2	3	0	1	0	1				
Neodrepanis coruscans					9	9	9	27								
Neodrepanis hypoxantha													7		9	16
Coracina cinerea	4	2	3	9	4	4	2	10	3	5	3	11				
Phyllastrephus madagascariensis	4	4	8	16	2	0	2	4	2	1	1	4				
Phyllastrephus zosterops	2	3	4	9												
Phyllastrephus cinereiceps					0	1	3	4	0	1	3	4				
Hypsipetes madagascariensis	12	11	9	32	3	5	4	12	5	3	6	14	5		7	12
Saxicola torquata	1	5	4	10									1		0	1
Copsychus albospecularis					6	4	4	14	4	6	3	13	9		8	17
Pseudocossyphus sharpei					2	5	4	11	11	9	10	30	15		20	35
Nesillas typica					9	7	8	24	3	3	3	9				
Dromaeocercus brunneus	1	0	0	1	5	5	5	15	6	4	3	13				
Newtonia amphichroa	0	1	0	1	7	5	8	20	6	7	5	18	8		5	13
Newtonia brunneicauda	9	9	9	27	8	8	8	24					2		5	7

TABLE 8-7. Continued.

Species	Elevational zone*														
	875 m				1260 m				1550 m				1950 m		
	R	S	V	T	R	S	V	T	R	S	V	T	R	V	T
Neomixis tenella	1	5	3	9	2	0	0	2							
Neomixis viridis	7	8	6	21	3	4	7	14	1	1	4	6			
Neomixis striatigula	5	8	8	21	5	9	6	20	1	2	0	3			
Cryptosylvicola randrianasoloi					4	8	4	16	10	9	6	25	9	7	16
Pseudobias wardi	0	1	0	1	1	3	3	7	1	1	0	2			
Terpsiphone mutata	6	11	3	20	5	4	6	15	0	0	2	2			
Oxylabes madagascariensis	2	2	0	4	2	1	4	7	0	1	1	2			
Mystacornis crossleyi	2	3	1	6	1	4	4	9							
Crossleyia xanthophrys									1	0	2	3			
Nectarinia souimanga	12	10	11	33	19	14	13	46	10	10	12	32	14	14	28
Nectarinia notata	4	4	4	12	1	4	3	8	1	1	0	2	2	2	4
Zosterops maderaspatana	5	7	8	20	5	6	7	18	5	5	4	14			
Calicalicus madagascariensis	10	9	5	24	3	4	6	13							
Schetba rufa	3	10	4	17	0	0	1	1							
Vanga curvirostris	2	0	0	2											
Leptopterus viridis	2	1	2	5	1	6	4	11	0	1	0	1			
Leptopterus chabert	0	0	4	4	0	0	1	1							
Cyanolanius madagascarinus	5	6	2	13	1	5	4	10							
Euryceros prevostii	1	1	3	5	0	0	1	1							
Tylas eduardi	0	2	0	2	1	2	1	4							
Dicrurus forficatus	6	6	3	15	6	2	5	13							
Ploceus nelicourvi	0	1	1	2	2	0	3	5	0	0	2	2			
Foudia omissa	5	1	0	6	0	1	0	1	3	5	4	12	2	3	5
Foudia madagascariensis	2	2	0	4	0	0	1	1	0	1	0	1			
Total species	37	42	35	49	40	34	44	47	24	26	23	32	16	14	16

* R = ridge; S = slope; V = valley; and T = total.

TABLE 8-8. Density estimates of species recorded more than 15 times within a single elevational zone.

Species	Elevational zone				Pooled estimates (samples pooled)
	875 m	1260 m	1550 m	1950 m	
Coua caerulea	183.17 (50.98–658.13)				
Atelornis crossleyi		43.09 (20.79–89.30)		66.52 (34.95–126.5)	54.64 (36.76–81.22) (1260,1550, 1950 m)
Neodrepanis coruscans†		1,192 (852–1,167)			
Neodrepanis hypoxantha†				3,529.9 (1,914–6,508)	2,650 (1,640–4,281) (1550, 1950 m)
Phyllastrephus madagascariensis	67.83 (43.74–105.21)				
Hypsipetes madagascariensis	116.94 (71.86–190.30)				
Pseudocossyphus sharpei				212.7 (112.5–402.0)	142.6 (94.09–216.3) (1260, 1550, 1950 m)
Nesillas typica		267.81 (141.98–505.18)	1,807.2 (843.25–3,873)	1,547.00 (1,044.60–2,291.1)	
Dromaeocercus brunneus		56.26 (31.25–101.28)			49.52 (31.16–78.69) (1260, 1550 m)
Newtonia amphichroa		243.18 (123.21–479.94)			168.6 (111.7–254.0) (1260, 1550. 1950 m)
Newtonia brunneicauda	294.52 (70.00–1,247)	612.10 (217.12–1,725.7)	170.51 (86.43–336.40)		
Neomixis viridis	180.10 (109.42–296.42)				
Neomixis striatigula	32.52 (12.97–81.56)	32.45 (15.41–68.38)			
Cryptosylvicola randrianasoloi		21.31 (10.01–45.36)	135.87 (30.12–612.83)	66.51 (34.95–126.60)	100.2 (43.42–231.32) (1260, 1550, 1950 m)
Terpsiphone mutata		315.60 (54.94–1,812.9)			
Nectarinia souimanga	226.75 (143.13–359.23)	726.08 (453.70–1,162.0)	857.94 (581.08–1,266.7)	568.13 (362.33–890.82)	

Species	Elevational zone				Pooled estimates (samples pooled)
	875 m	1260 m	1550 m	1950 m	
Zosterops maderaspatana	146.83 (97.14–221.93)	452.92 (294.36–696.89)			
Calicalicus madagascariensis	108.21 (8.21–1,424.9)				
Schetba rufa	34.65 (20.44–58.74)				
Dicrurus forficatus	66.05 (15.94–273.68)				

* Density estimates were calculated with the DISTANCE program (Laake et al., 1993). Values are the number of individuals per square kilometer; 95% confidence intervals appear in parentheses. Calculation of pooled density estimates is described in the text (see p. 96).
† Densities for *Neodrepanis* spp. are almost certainly exaggerated (see p. 112).

Bird Mass Data

Mist-netting resulted in the capture of 204 individuals of 24 species (Table 8-4). Table 8-9 presents data on masses of the birds captured.

Mixed-Species Flocks

From their observed foraging behavior and diet, the 54 forest species (excluding raptor, nocturnal, and aerial species) recorded during 160 hr of strip census counts were classified into four guilds:

1. 14 terrestrial species, feeding mostly on the ground or in low, dense vegetation: *Lophotibis cristata, Mesitornis unicolor, Canirallus kioloides, Coua serriana, Coua reynaudii, Brachypteracias squamiger, Atelornis crossleyi, Copsychus albospecularis, Pseudocossyphus sharpei, Oxylabes madagascariensis, Crossleyia xanthophrys, Mystacornis crossleyi, Nesillas typica,* and *Dromaeocercus brunneus.*

2. 12 arboreal insectivores, slow searchers of foliage and branches or flycatchers, securing prey mostly by strikes or sallies: *Cuculus rochii, Coua caerulea, Centropus toulou, Brachypteracias leptosomus, Leptosomus discolor, Coracina cinerea, Pseudobias wardi, Terpsiphone mutata, Schetba rufa, Leptopterus chabert, Tylas eduardi,* and *Dicrurus forficatus.*

3. 18 arboreal insectivores, actively searching foliage, epiphytes, or bark and catching prey by gleaning, snatching, or probing: *Phyllastrephus madagascariensis, Phyllastrephus zosterops, Phyllastrephus cinereiceps, Randia pseudozosterops, Newtonia amphichroa, Newtonia brunneicauda, Neomixis tenella, Neomixis viridis, Neomixis striatigula, Hartertula flavoviridis, Cryptosylvicola randrianasoloi, Zosterops maderaspatana, Calicalicus madagascariensis, Hyposotta corallirostris, Leptopterus viridis, Cyanolanius madagascarinus, Oriolia bernieri,* and *Ploceus nelicourvi.*

4. 10 mostly nectarivorous, granivorous, or frugivorous species: *Alectroenas madagascariensis, Treron australis, Coracopsis nigra, Philepitta castanea, Neodrepanis coruscans, Hypsipetes madagascariensis, Nectarinia souimanga, Nectarinia notata, Foudia omissa,* and *Foudia madagascariensis.*

The relative proportions of the last three categories did not vary significantly between the 875 m and 1260 m elevational zones (Table 8-10 and χ^2 tests, $p < 0.10$ in Table 8-11). Only the species feeding on or just above the ground (guild 1) were

TABLE 8-9. Mass of birds netted during the survey of the RS d'Anjanaharibe-Sud.

Species	n	Mass (g)		
		Minimum–maximum*	Mean	SD
Streptopelia picturata	2	208.5, 196.5		
Otus rutilus	4	95.0–107.5	100.5	5.21
Ispidina madagascariensis	1	19.0		
Atelornis crossleyi	2	79.0, 85.0		
Philepitta castanea	13	29.5–40.0	36.8	3.24
Neodrepanis coruscans	5	6.2–9.0	7.2	1.21
Neodrepanis hypoxantha	12	6.0–8.0	7.5	0.64
Phyllastrephus madagascariensis	7	19.5–32.0	28.7	5.50
Phyllastrephus zosterops	8	18.5–21.5	19.9	1.43
Phyllastrephus cinereiceps	7	13.0–21.5	18.4	3.27
Hypsipetes madagascariensis	6	38.0–46.5	43.4	2.90
Copsychus albospecularis	10	22.0–25.5	23.7	1.25
Pseudocossyphus sharpei	5	25.0–31.0	27.9	2.25
Nesillas typica	30	16.0–23.5	19.0	1.57
Dromaeocercus brunneus	1	14.0		
Newtonia amphichroa	11	11.0–16.5	13.7	1.50
Terpsiphone mutata	12	12.0–15.5	13.7	0.89
Oxylabes madagascariensis	7	21.5–28.0	24.9	2.42
Nectarinia souimanga	8	7.0–9.0	7.9	0.62
Nectarinia notata	1	13.5		
Zosterops maderaspatana	2	8.5, 12.0		
Ploceus nelicourvi	6	21.5–27.5	24.4	2.42
Foudia omissa	27	14.5–24.5	19.6	2.19
Foudia madagascariensis	6	14.5–17.5	16.3	1.03

* In cases in which fewer than three measurements are available, only the masses themselves are given.

significantly more abundant ($\chi^2_1 = 4.62, p < 0.05$) at the upper level. This numerical difference was also reflected in the rate of species turnover. Ten species (77%) in guild 1 were restricted to the lower zone (*Lophotibis cristata, Mesitornis unicolor, Canirallus kioloides, Coua serriana, Centropus toulou,* and *Brachypteracias squamiger*) or to the upper elevational level (*Atelornis crossleyi, Nesillas typica, Dromaeocercus brunneus,* and *Crossleyia xanthophrys*), whereas among the three arboreal bird guilds, only eight species (20%) occurred mainly, if not exclusively, either at the lower (*Treron australis, Schetba rufa,* and *Oriolia bernieri*) or upper level (*Neodrepanis coruscans, Phyllastrephus cinereiceps, Pseudocossyphus sharpei, Randia pseudozosterops,* and *Hartertula flavoviridis*).

Discussion

Methodological Considerations

POINT COUNTS—Rain forest point-count methodology has not been fully refined (Bibby et al.,

1992). Therefore, the implications of variation in two parameters were examined in the current study, the physical distance between point-count sample sites and the number of repeated visits made to each site.

In forest environments, point-count sample sites should be at least 100 m apart (Recher, 1981) in order to minimize double counts of individual birds, and other studies in the tropics have used distances of up to 300 m (Recher, 1981; Bibby et al., 1992; Putnam & Goodman, in prep.). Thus, the 125 m distance used in this study was at the low end of the range.

Double counts were relatively easy to detect in this study because a note was made of the distance and direction of loudly calling birds at each point-count site. Any contact from subsequent point-count sites along the path that was in a direction to be expected from a contact at the previous site was bracketed when noted and was not used in data analysis. In addition, any single bird that was heard calling continuously during the periods of both adjacent point counts, as well as during the period spent traveling between the two sites, was noted only for the first point-count site.

The number of data points eliminated by the first procedure was low, only 45 of a total of 2,820 bird contacts (1.6%). Thus, the error rate caused by double counting on adjacent point-count sites was low. Furthermore, densities calculated from contact frequencies of loudly calling species were imprecise because most contacts fell into the +200 m distance band.

A more serious potential problem with point-count sites separated by 125 m and sampled on more than one occasion is that birds might move between point-count sites (Buckland et al., 1993). Densities in the present study were calculated using the single maximum count from five repeated samples at a point-count site. If individual birds move between point-count sites during the sampling at an elevational zone, it is possible that an individual bird could be incorporated into maximum counts at two different point-count sites sampled on different days. The importance of this error is not known.

The advantage of conducting point counts at sites separated by 125 m is that it is possible to have more samples in a limited area than if the intersite distance is 200 or 300 m. Because few trails existed in the surveyed area before this inventory, particularly at the upper elevations, and because within most zones 1–2 days were spent cutting trails, a shorter intersite distance was advantageous.

Because only the maximum count of any one species from any one of the five samples was used in density calculation, all other contacts made of that species at that point-count site were redundant. Figure 8-2 shows the percentage redundancy in each elevational zone. Around 50% of all contacts made over the five samples from each point-count site are unusable for density calculation purposes. The proportion of unusable data per sample drops slightly with elevation, although the reason for this is unclear. Replacing repeated point-count samples with new, independent samples would reduce the proportion of unusable data. However, this would require more time in trail preparation. In future surveys the balance made between these two conflicting variables will depend on the manpower available to cut trails and the time available in each elevational zone.

A potential advantage of conducting five repeated samples at each point-count site (over a strategy using fewer repeated samples) is that there is an increased likelihood of sampling all the species present at a point-count site. To examine this possibility, for each point-count site within an
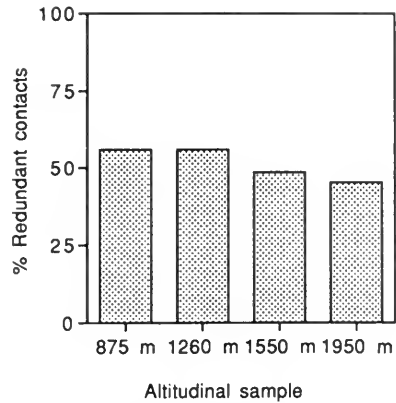
FIG. 8-2. Percentage redundancy (number of data points used in density calculations divided by total number of data points collected at each elevational zone) in four elevational zones in the RS d'Anjanaharibe-Sud.

elevational zone, mean species-accumulation curves were plotted (Fig. 8-3). These show clearly that there is little evidence of flattening after five repeated samples and that after five samples the number of species detected at a point-count site was more than double that detected after a single sample.

A further question of interest to sampling strategy is the representativeness of samples within an elevational zone. If a single point-count site were to hold most of the species present within an elevational zone, then few samples would be required per elevational zone to fully represent the bird community of the zone. This question was addressed by calculating the relationship between the number of species detected in the elevational zone as a whole and the mean number of species detected after each repeated sample at an individual point count site. This relationship is expressed as a mean percentage of the total species found over the elevational zone, shown in Figure 8-3. For all elevational zones except 1950 m, even after five repeated samples at each point-count site, a mean of less than 40% of the total elevational zone species list was detected at a point-count site.

These observations might be explained in two ways. First, bird distributions could be patchy within elevational zones, so that a point-count sample site was unlikely to hold more than 50% of bird species in the elevational zone. However, if this were the case, one would expect to see some flattening of the curves in Figure 8-3, which is not the case. In addition, relatively few species of bird at any elevation show contact frequencies

TABLE 8-10. Total number of foraging birds visually recorded within 20 m on either side of understory forest trails between 05:30 and 16:30 during the same time (80 hr) in two nearby elevational zones in the RS d'Anjanaharibe-Sud, associated with or outside mixed-species flocks of foraging insectivores.

| Species | Elevational zone | | | | Foraging niche* |
| | 750–950 m | | 1150–1350 m | | |
	In flocks	Outside of flocks	In flocks	Outside of flocks	
Lophotibis cristata		3			SE, lit, pro
Mesitornis unicolor		2		1	SE, lit, pro
Canirallus kioloides		5			AC, lit, gle
Alectroenas madagascariensis		11		11	F
Treron australis		1			F
Coracopsis nigra		20		22	F
Cuculus rochii		2	1	3	SE, fol, gle
Coua serriana		2			SE, lit, gle
Coua reynaudii		2		7	SE, bar, gle
Coua caerulea	3	16	2	17	SE, fol, gle
Centropus toulou		3			SE, fol, gle
Brachypteracias leptosomus		1		3	SE, fol, gle
Brachypteracias squamiger		3			SE, lit, gle
Atelornis crossleyi				4	SE, lit, gle
Leptosomus discolor		2	1	4	SE, fol, gle
Philepitta castanea	8	2	5	5	F
Neodrepanis coruscans			2	10	F
Coracina cinerea	16	5	10	6	SE, fol, str
Phyllastrephus zosterops	4	26	2	6	AC, fol, gle
Phyllastrephus madagascariensis	4	5	3	1	AC, fol, gle
Phyllastrephus cinereiceps		1	6	10	AC, fol, gle
Hypsipetes madagascariensis	19	60	11	25	F
Copsychus albospecularis		2		7	SE, bar, gle
Pseudocossyphus sharpei		2	2	14	SE, lit, pro
Nesillas typica		1	2	49	AC, fol, gle
Dromaeocercus brunneus				1	AC, fol, gle
Randia pseudozosterops		1		2	AC, bar, pro
Newtonia amphichroa	2	2	3	13	AC, fol, gle
Newtonia brunneicauda	67	35	22	42	AC, fol, gle
Neomixis spp.†	39	10	33	19	AC, fol, gle
Hartertula flavoviridis		1	6	8	AC, fol, gle
Cryptosylvicola randrianasoloi			5	11	AC, fol, gle
Pseudobias wardi		3	3	7	SW, fol, sal
Terpsiphone mutata	17	11	11	9	SW, fol, sal
Oxylabes madagascariensis		3		1	AC, lit, gle
Crossleyia xanthophrys				5	AC, lit, pro
Mystacornis crossleyi		3		3	AC, lit, pro
Zosterops maderaspatana	84	40	51	49	AC, fol, gle
Nectarinia notata	3	3			N
Nectarinia souimanga	13	20	15	83	N
Schetba rufa	1	5			SE, fol, str
Calicalicus madagascariensis	16	8	9	13	AC, fol, gle
Leptopterus viridis	8		5	1	AC, fol, str
Leptopterus chabert	2	2		4	SE, fol, str
Cyanolanius madagascarinus	19	3	9	1	AC, fol, gle
Oriolia bernieri	2				AC, fol, gle
Hypositta corallirostris	4		4		AC, bar, pro
Tylas eduardi	3		10	2	SE, fol, str

TABLE 8-10. *Continued.*

| | Elevational zone | | | | |
| | 750–950 m | | 1150–1350 m | | |
Species	In flocks	Outside of flocks	In flocks	Outside of flocks	Foraging niche*
Dicrurus forficatus	34	10	15	11	SW, fol, sal
Ploceus nelicourvi	5		8	1	AC, fol, gle
Foudia spp.‡		7		3	F

* For details of foraging niche, see text and Table 8-2. Information is given in the following order: foraging method (AC = active searcher; SE = slow searcher; and SW = sit and wait), foraging sites (lit = litter and near-ground vegetation; bar = bark and epiphytes, on trunks and branches; and fol = on or near foliage, dead leaves, vines, and twigs), and capture techniques (gle = glean, snatch, and hoverglean; pro = probe, tear, and peck; str = strike, pounce, and sally glean; and sal = sally and fly-catch). Mostly nectarivorous (N) or frugivorous (F) diets may include some arthropods. Only the dominant site and technique are cited (≥50% of field records).

† *Neomixis tenella, N. viridis,* and *N. striatigula* pooled.

‡ *Foudia madagascariensis* and *F. omissa* pooled.

that differ markedly between ridge, slope, and valley samples within one elevational zone (Table 8-7). Thus, bird distribution does not appear to be particularly patchy on the local or elevational zone scale.

Alternatively, it is possible that even after five repeated point-count samples, fewer than half the species present at some time over the survey period at a point-count site had been detected. This might be the result of variation over time in the detectability of certain species resident at a site, possibly because some species have relatively quiet songs but large territories. Alternatively, species may be relatively mobile, and the same individual birds may be detectable from more than one point-count site over a period of several days. If true, this has important implications for the calculation of density estimates, because the use of the maximum number of contacts per point-count site for density calculation may mean

TABLE 8-11. Distribution of the main feeding guilds between birds recorded in the two elevational levels, then among all birds pooled, between those associated with mixed flocks and those foraging alone, in pairs, or in family groups.

| | % All individuals recorded | | | |
Guild	750–950 m	1150–1350 m	In flocks	Outside of flocks
Terrestrial	3.8	10.9	0.6	12.5
Slow searchers	19.1	17.7	20.5	16.8
Active gleaners	53.8	45.8	66.8	36.9
Frugivores	23.3	25.6	12.1	33.8
Total	717	750	629	838

that density estimates are calculated using a high percentage of duplicate contacts with the same individual birds, and overestimates of density will result. This issue is discussed in more detail below.

We learned three important lessons from this analysis: (1) The number of repeated point-count samples for density assessment in Malagasy rain forest should be less than five, probably no more than three, to reduce the level of redundant data and to reduce the possibility of duplicate contacts with mobile birds. (2) For density analysis, effort should be made to maximize the number of point-count sites rather than maximizing the number of repeated samples, if possible through development of an extensive trail system before sampling. (3) Especially in areas with high species diversity, the presence or absence of contacts with a species at a point-count site, even after five repeats, may not be a realistic indicator of the species' actual presence or absence at that point. More data are required on the seasonality of vocalization by individual bird species and the mobility and territory sizes of forest birds to clarify the explanation for this. Thus, point counts may not be an efficient method for assessing the local distribution of birds in different habitats within an elevational zone, nor for assessing the overall diversity of species within the whole elevational zone.

PROBLEMS WITH DENSITY CALCULATIONS—Two potential problems arose in data analysis. The first is that if (as in this case) only the maximum number of contacts made over five repeated samples at each point-count site are made, an overestimation of the density of mobile species is possi-

FIG. 8-3. Cumulative percentage of total number of species recorded on point counts in four elevational zones, over five repeated samples in each zone, in the RS d'Anjanaharibe-Sud.

ble. This overestimate occurs because for adjacent point-count samples, maximum contact numbers over the five repeats would rarely be expected to occur on the same day. In a hypothetical example, a population of birds might consist of a single resident individual near each of 10 adjacent sample sites and three mobile individuals of the same species. If these mobile individuals moved along the line of adjacent sample sites over the period during which the five repeated samples were made, then it is theoretically possible that four individuals (three mobile and one resident) could be recorded at each of the 10 adjacent sample sites. Thus, density calculations would be based on 40 contacts, and density estimates would undoubtedly be much higher than the 13 individuals actually present. In reality, individuals of most species probably move over a larger home range than 150 m, so this error undoubtedly occurs, but its magnitude is difficult to assess. By making fewer repeated samples at each point count site, this error could be minimized.

The second major potential error associated with the survey results relate to estimates calculated for *Neodrepanis* spp. These two species often approached the observer while point counts were in progress. This violates a fundamental assumption of point-count methodology, i.e., that the sampled organism does not move in response to the observer before it is detected (Buckland et al., 1993). In addition, the calls of this genus are soft and, although easy to detect at close range, could not be heard at more than about 50 m. Thus, it is quite possible that birds approached the observer from 100 m or more, becoming detectable only at 10 m or 20 m range. For this reason the

density estimates for these two species (Table 8-8) are almost certainly exaggerated.

Comparative Effectiveness of Survey Techniques

Active searching contributed most to the species accumulation curves, and other techniques were relatively inefficient at detecting species. Only 67 (79%) of 84 species occurring in forest were found on point counts, and only 24 of 84 (29%) of these species were found by mist-netting. No species was detected only on point counts or by mist-netting. The species not detected by point counting included seven raptors, two nocturnal species, five aerial feeders, and two scarce forest-floor feeders (*Mesitornis unicolor* and *Dryolimnas cuvieri*). This pattern fits with previous observations about the limitations of point counts (Bibby et al., 1992). Only three forest passerines were not detected on point counts: *Hartertula flavoviridis*, *Hypositta corallirostris*, and *Hartlaubius auratus*. The first two species, limited to forest, were rather scarce at the RS d'Anjanaharibe-Sud, being detected in only one elevational zone each (1250 m and 875 m, respectively). The third species is generally more detectable outside forest.

Contact frequency is often used as an index of species abundance (e.g., Thorstrom & Watson, 1994), but this study shows that although point counts are time consuming, they provide information not otherwise available through contact frequency. Table 8-5 shows that valley forest samples had significantly fewer species and fewer

contacts than ridge forest at 875 m. This result contrasts with the higher density of birds in valley forest than either ridge or valley forest at the same elevation and suggests that although more contacts may be made on ridges, many of them are of birds detectable at long ranges. Thus, in this instance, point counts convey a different message than one would infer from relative abundance measures derived from contact rates. The extra time and effort involved in point counts have produced inferences useful for conservation that could not have been obtained from encounter rate data.

The call-playback technique was not useful. This technique was effective for detecting *Mesitornis variegata* in western Madagascar (Hawkins, 1994), so its lack of results here, particularly for *Mesitornis unicolor*, is surprising. It may be that the peak song period for some species was missed or that several species occur in very low densities.

Comparisons with Other Rain Forest Inventories

A total of 94 bird species were recorded within the reserve (Table 8-2). Of these, 84 (92%) are species found regularly within forest. This compares with (from north to south, forest species in more or less complete inventories only) 84 recorded at the RNI de Marojejy (400–2173 m; Safford & Duckworth, 1990), 74 on the Masoala Peninsula (0–1100 m; Thorstrom & Watson, 1994), 72 at RS d'Ambatovaky (380–1200 m; Thompson & Evans, 1991), 85 at RNI de Zahamena (Thompson, 1987; Goodman, unpubl. data; Hawkins, unpubl. data), 84 at RS d'Analamazaotra-Périnet and PN de Mantadia and Maromiza (Nicoll & Langrand, 1989; Hawkins, pers. obs.), 81 at PN de Ranomafana (Zack, pers. comm.), and 73 at RNI d'Andringitra (Goodman & Putnam, 1996). Thus, the bird species diversity in the RS d'Anjanaharibe-Sud is relatively rich compared with other sites in Malagasy humid forest.

Relationships between Species Distribution over Microhabitats and Vegetation Structure

Of 67 species recorded on point counts, only nine species (13%) showed contact frequencies that differed markedly between microhabitats within an elevational zone (Table 8-7). Although there was significant variation between the vegetation structure at sample sites on ridges and in valleys at all elevational levels, explanation of variation in bird community patterns should be attempted only if the relationships are clear and ecologically interpretable. An example of this might be a shrub-layer feeder that was found more commonly on ridges (where the shrub layer is denser) in more than one elevational zone. In this case, it is difficult to account for the distributions of the nine species by using variation in vegetation structure. None of the nine species have asymmetric distributions in one elevational zone that are matched by a similar distribution in an adjacent sample; indeed, all nine species have asymmetric distributions in only one elevational zone. The nine species belong to six different guilds, and of the same-guild species groups (*Coua reynaudii* and *Atelornis crossleyi*, both terrestrial frugivore insectivores, and *Cuculus rochii*, *Neomixis viridis*, and *Newtonia brunneicauda*, all gleaning insectivores), there are only two with similar distributions; both *Neomixis viridis* and *Newtonia brunneicauda* are more common in valleys, although the first species shows this distribution at 1550 m and the second at 1950 m. Because *Newtonia brunneicauda* often feeds in the shrub layer, which is denser on ridges than in valleys, this observation is difficult to explain ecologically.

Overall, it is difficult to be confident that these distributions are other than random. A more efficient method of determining species habitat preferences would have been to concentrate observations on a particular species; in order to increase sample sizes. A similar conclusion can be made about the relationship between greater canopy height in valleys and a higher overall density of birds in valleys at 875 m compared with ridges and slopes. This pattern reflects observations made elsewhere in the world that taller forests are often more structurally complex than low forests and as a result may support a greater density or diversity of birds (Terborgh, 1977; Cody, 1985). However, such a conclusion is not clearly supported by observations at other elevational zones, where canopy height is also higher in valleys than on ridges (Table 8-6), but overall bird density is no different from that found elsewhere.

Elevational Variation in the Bird Community

Rand (1936, p. 243) stated that "most [eastern rain forest] species were not governed by altitude

to any great extent." Salomonsen (1934a,b) indicated that a few species of Malagasy bird appeared to have montane subspecies but did not detail any species turnover with altitude. However, Safford and Duckworth (1990) suggested that in the RNI de Marojejy, many species showed a distribution that changed significantly around 1000–1200 m, and a similar pattern was demonstrated for the RNI d'Andringitra (Goodman & Putnam, 1996). In the RS d'Ambatovaky (Thompson & Evans, 1991) and on the Masoala Peninsula (Thorstrom & Watson, 1994), the bird communities show some elevational zonation.

Species that in these studies appear to show elevational limitation or to be more common at certain elevations across their ranges include *Brachypteracias squamiger, B. leptosomus, Coua serriana, Schetba rufa,* and *Euryceros prevostii* below 1000 m and *Atelornis crossleyi, Neodrepanis hypoxantha, Phyllastrephus cinereiceps, Pseudocossyphus sharpei,* and *Crossleyia xanthophrys* above 1000–1200 m.

In this study, the three major parameters of bird community composition investigated were species number (overall species recorded and species recorded per point count), contacts per point count (a measure of abundance), and overall density. Figure 8-4A shows that species number declined in an approximately linear manner with elevation; the 875 m zone falls slightly off the trend, having slightly fewer species.

Rahbek (1995) criticizes some studies of elevational variation in species richness for not considering sample area as a factor in determining species richness. Survey sample area within elevational bands may decrease with elevation owing to increasing slope at high elevations, and because species richness may be strongly related to the surface area sampled, studies on variation in species richness should adjust values at high elevations according to the surface area sampled.

In this study, more sampling effort was made at lower elevations than at higher ones (Table 8-1), mostly because of the larger surface area available for sampling. Although searches were made for birds outside the area used for point-count sampling, the number of point-count samples made in each elevational zone provides an index of surface area sampled. Figure 8-4B shows the species richness data adjusted according to the number of point-count samples made at each elevation. The effect of adjustment for sample area on species richness is to reduce the effect of elevation. The first three altitudinal samples are sim-
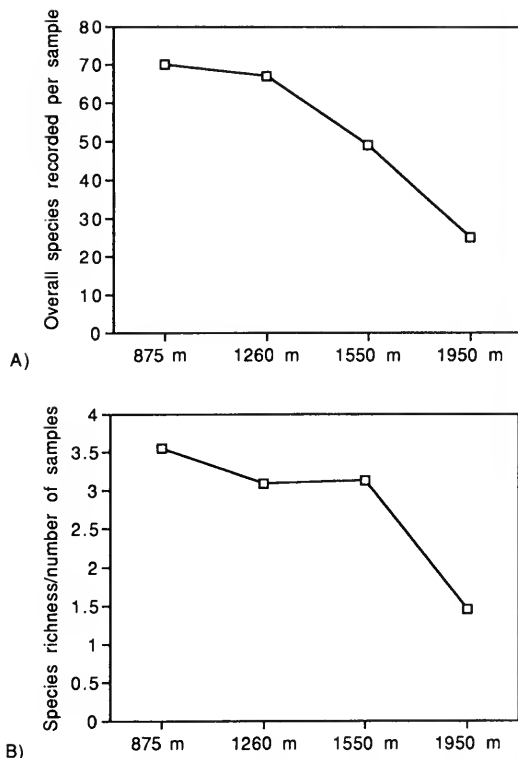
Fig. 8-4. Variation in (**A**) overall number of species recorded with elevation in the RS d'Anjanaharibe-Sud and (**B**) in sample area-adjusted species richness with elevation (for adjustment calculation, see p. 114).

ilar, with only the highest elevation sample showing distinctly lower adjusted species richness. Another possible method of adjusting for sample size (used here as an index of surface area sampled) is to compare the mean number of species and individuals recorded per point-count sample (over the five repeats at each sample) with elevation.

Figure 8-5A shows that variation with elevation of mean maximum species number and contact frequency per point-count sample follow a similar pattern to that found with overall number of species (Fig. 8-4A). The number of species per sample increased between 875 and 1250 m. This suggests that sample sites at 1250 m were more uniform in species composition than those at 875 m since species diversity was higher at 875 m than at 1250 m. This is supported by the observation that densities of birds were significantly different between habitats at 875 m, whereas densities were similar in all habitats at 1250 m (Table 8-5).

Figure 8-5B shows that the bird density estimate is considerably higher at 1260 than at 875
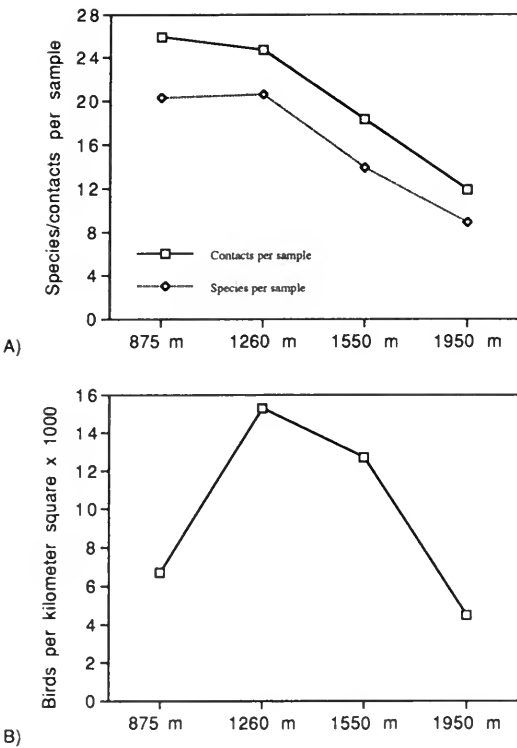
Fig. 8-5. Variation in (**A**) mean maximum species number and contact frequency per point-count sample with elevation in the RS d'Anjanaharibe-Sud and (**B**) overall bird density with elevation. The values for the 875 and 1950 m samples are the means of habitats with significantly different densities (Table 8-5).

m. Estimates of densities at 1250 and 1550 m are not significantly different (Table 8-5). Density is significantly higher at 1550 than at 875 m. This result is in striking contrast to the finding that contact frequencies with birds are slightly higher at 875 m than at 1250 m (Fig. 8-5A) and suggests that many contacts with birds at 875 m were at long distance. It also suggests that contact data from different species are unreliable estimators of relative density.

Although these observations may be the results of differences in absolute bird densities, there are other potential explanations. For example, the breeding season for birds in the RS d'Anjanaharibe-Sud was already well under way by mid-October, and it is possible that several species were singing less regularly at 875 m than at 1250 m because the breeding season was further advanced at the lower camp. However, the sequence of sampling (lower camps were visited first) would tend to have reduced this effect.

Patterns of Species Occurrence with Elevation

Eight basic patterns of elevational distribution can be inferred from point-count contact frequencies (Table 8-7). These are displayed in Figure 8-6A–H. For the sake of clarity, species are considered to be either present in at least moderate abundance in an elevational zone or absent or very scarce compared with other elevational zones. For some species, other casual observations have been taken into account, e.g., for secretive birds not easily detected on point counts. Only species identified in Table 8-2 as forest-occurring species were used in this analysis. Raptors were not included because they are treated separately (Chapter 9).

Fifty-eight of the 84 forest species were treated in this analysis. The remaining species include rarely seen raptors, nocturnal species, aerial species, and rarely seen forest species. Figure 8-6A–H shows that the majority of forest species have distributions that vary across the range of elevations sampled. Of the 60 species treated in the analysis, 30 did not occur regularly at or above 1550 m, and eight did not occur regularly below 1250 m. Only eight species (Fig. 8-6H) appeared to have regular distributions across all elevational zones.

Species Replacement

Only two genera (*Neodrepanis* and *Phyllastrephus*) have species that appear to replace each other with elevation. In addition, members of two families (Turdidae: *Copsychus albospecularis* and *Pseudocossyphus sharpei*; and Sylviidae: *Neomixis tenella*, *Neomixis striatigula*, and *Cryptosylvicola randrianasoloi*) are similar enough in size and habits to suggest that they might replace each other with elevation. In all these cases of apparent species replacement, further ecological and behavioral studies are required to establish the existence of presumed competition.

Neodrepanis coruscans and *N. hypoxantha* appear to provide the clearest example of species replacement with elevation. There was no site where the two species occurred sympatrically. On the basis of morphology and feeding behavior, they are likely to compete for food resources.

Phyllastrephus madagascariensis and *P. zosterops* were both common at 875 and 1250 m, whereas *P. cinereiceps* was common only at 1250 and 1550 m. Superficially, these three species re-
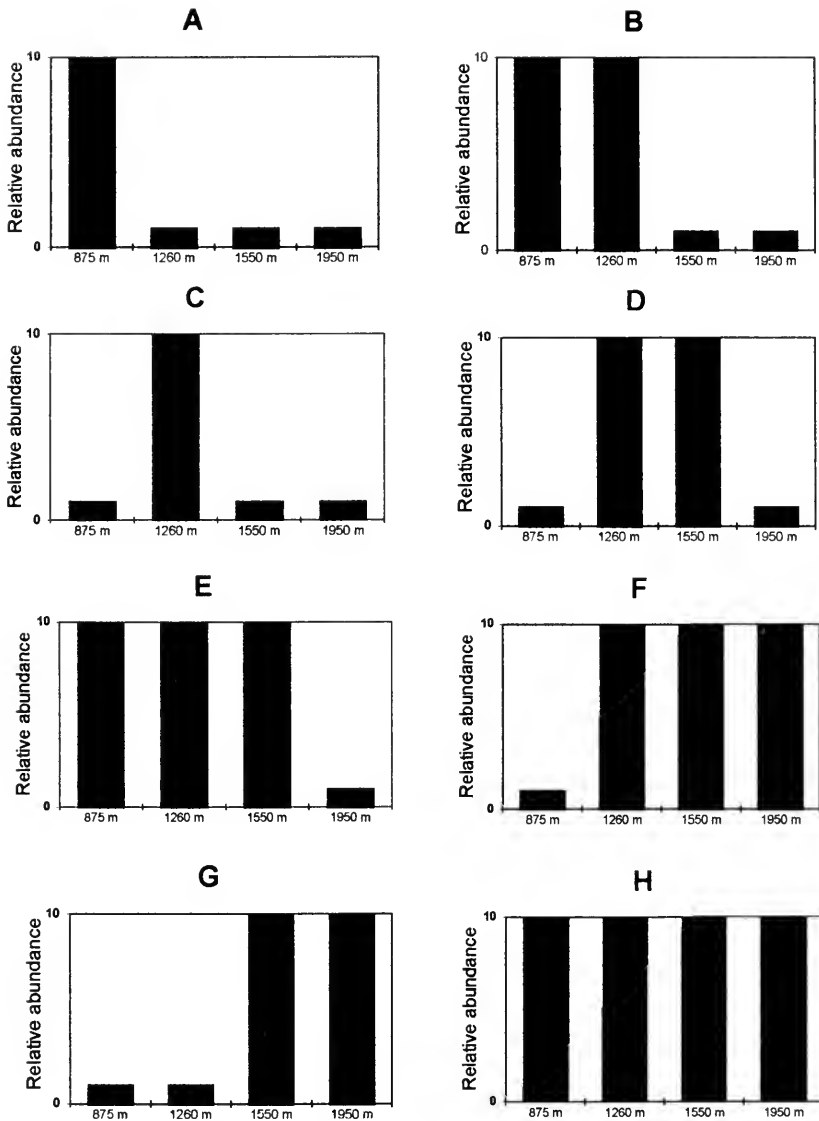
FIG. 8-6. Indices of relative measures of bird abundance based on point-count sampling. Index values: 1 = relatively rare or absent and 10 = relatively abundant. **A**, Low-elevation specialists: *Mesitornis unicolor, Treron australis, Coua serriana, Brachypteracias squamiger, Neomixis tenella, Mystacornis crossleyi, Vanga curvirostris, Schetba rufa,* and *Euryceros prevostii.* **B**, Low- to midelevation specialists: *Canirallus kioloides, Cuculus rochii, Centropus toulou, Brachypteracias leptosomus, Phyllastrephus madagascariensis, Phyllastrephus zosterops, Copsychus albospecularis, Randia pseudozosterops, Neomixis striatigula, Pseudobias wardi, Nectarinia notata, Calicalicus madagascariensis, Leptopterus chabert, Cyanolanius madagascarinus, Hypositta corallirostris, Dicrurus forficatus,* and *Foudia madagascariensis.* **C**, Lower midelevation specialists: *Neodrepanis coruscans* and *Hartertula flavoviridis.* **D**, Midelevation specialists: *Phyllastrephus cinereiceps* and *Crossleyia xanthophrys.* **E**, Species not present at upper elevation: *Lophotibis cristata, Sarothrura insularis, Alectroenas madagascariensis, Coua caerulea, Leptosomus discolor, Philepitta castanea, Coracina cinerea, Newtonia brunneicauda, Neomixis viridis, Terpsiphone mutata, Oxylabes madagascariensis, Leptopterus viridis, Tylas eduardi,* and *Ploceus nelicourvi.* **F**, Mid- to high-elevation specialists: *Atelornis crossleyi, Pseudocossyphus sharpei, Nesillas typica, Dromaeocercus brunneus, Newtonia amphichroa,* and *Cryptosylvicola randrianasoloi.* **G**, High-elevation specialists: *Neodrepanis hypoxantha* and *Saxicola torquata.* **H**, Uniformly distributed species: *Buteo brachypterus, Coracopsis nigra, Coua reynaudii, Streptopelia picturata, Hypsipetes madagascariensis, Nectarinia souimanga, Zosterops maderaspatana,* and *Foudia omissa.*

TABLE 8-12. Foraging guild (excluding predators) presence in elevational distribution types.

Elevational distribution type	Guild*									Total
	TI	TIF	TF	AF	SGI	SI	GI	ANI	GI/F	
Low elevation specialists	0	4 (44%)	0	1 (11%)	3 (33%)	0	1 (11%)	0	0	9
Low and lower midelevation specialists	1 (6%)	1 (6%)	1 (6%)	0	1 (6%)	3 (18%)	9 (53%)	1 (6%)	0	17
Lower midelevation specialists	0	0	0	0	0	0	1 (50%)	1 (50%)	0	2
Midelevation specialists	1 (50%)	0	0	0	0	0	1 (50%)	0	0	2
Absent from high elevations	0	2 (15%)	0	2 (15%)	4 (31%)	1 (8%)	4 (31%)	0	0	13
Mid-high elevation specialists	1 (17%)	1 (17%)	0	0	0	0	0	4 (67%)	0	6
High elevation specialists	1 (50%)	0	0	0	0	0	0	1 (50%)	0	2
Uniform distribution	0	0	3 (43%)	2 (29%)	0	0	0	1 (14%)	1 (14%)	7
Total species	4 (7%)	7 (12%)	5 (9%)	4 (7%)	8 (14%)	4 (7%)	17 (29%)	8 (14%)	1 (2%)	58

* AF = arboreal frugivore; ANI = arboreal nectarivore/insectivore; GI = gleaning insectivore; GI/F = gleaning insectivore/frugivore; SGI = sally-gleaning insectivore; SI = sallying insectivore; TF = terrestrial frugivore (includes granivore); TI = terrestrial insectivore; TIF = terrestrial insectivore/frugivore (includes granivore).

semble each other in morphology, although *P. cinereiceps* is the smallest and shortest billed. Foraging observations of *P. cinereiceps* suggest that it favors foraging on tree trunks covered in moss, which are abundant at middle and higher elevations, whereas *P. zosterops* specializes on small understory shrubs, and *P. madagascariensis* in dense vegetation thickets (Thompson, 1987).

Copsychus albospecularis and *Pseudocossyphus sharpei* are similar in size and bill shape. Both are terrestrial and shrub-layer insectivores, and although they both occurred at the 1250 m elevational zone, it was unusual to find them both in the same area at this elevation. Only *Copsychus* was found at 875 m, and *Pseudocossyphus* occurred alone at 1550 and 1950 m.

Cryptosylvicola randrianasoloi is an arboreal gleaning insectivore that is absent from the 875 m zone. *Neomixis tenella* and *N. striatigula* were most common at 875 and 1260 m. *Cryptosylvicola randrianasoloi* resembles *N. striatigula* in behavior and bill morphology, although little is known of the feeding ecology of the two species.

Patterns of Guild Distribution

Table 8-12 shows the distribution of foraging guilds (noted for each species in Table 8-2)

among the types of elevational distribution identified in Figure 8-6A–H. Insectivores in general are the group that have the most restricted distributions. Species confined to the lower parts of the reserve are mostly terrestrial insectivores/frugivores, sally-gleaning insectivores, and gleaning insectivores. Few species are limited to the midelevation parts of the reserve. Most of the species absent from the highest elevations are gleaning and sally-gleaning insectivores. Generally, species distributed over a wide range of elevations are those with at least some fruit in the diet.

Community Variation with Elevation

Species richness appears to decline more or less linearly with elevation in the RNI de Marojejy (Safford & Duckworth, 1990) and RNI d'Andringitra (Goodman & Putnam, 1996), the only Malagasy rain forest sites to have had exhaustive inventories conducted at a range of elevations. However, at the first site at least, no attempt was made to correct species richness with survey effort.

In the RS d'Anjanaharibe-Sud, species richness is genuinely lower at 1950 m than elsewhere in the elevational sample (Figs. 8-4A,B, 8-5A). Whether species richness is lower at 1550 m than at 1250 or 875 m is unclear, as Figure 8-4B shows that varia-

TABLE 8-13. Patterns of records of foraging birds seen in the RS d'Anjanaharibe-Sud (see Table 8-10).

| Parameter measured | Elevational zone | | Statistical significance |
	750–950 m	1150–1350 m	
Mean no. of mixed flocks recorded per hour	0.33 (n = 26)	0.16 (n = 13)	$p < 0.01$*
Mean flock size (± SD)	14.42 ± 5.86	19.69 ± 11.93	NS†
Proportion of birds associated with mixed flocks‡	52.0–57.7%	32.9–35.9%	$p < 0.01$§
Mean number of birds recorded per hour	8.96	9.37	NS†

* Mann-Whitney U test.
† NS = nonsignificant.
‡ The first figure includes all species, and the second figure excludes large terrestrial and large frugivorous species, usually not members of mixed flocks (*Lophotibis* through *Leptosomus* in Table 8-10).
§ χ^2 test with Yates correction on the overall number of individuals and sign test on the direction of the difference within each species.

tion in species richness among these three sites can be accounted for, at least in part, by an index of the area surveyed. The species-accumulation curves (Fig. 8-1) suggest that in the areas surveyed there were few other species to be found at any of the elevational samples but do not indicate whether sampling over a wider area would have increased species richness at any one site. What does seem clear is that in the RS d'Anjanaharibe-Sud, some bird species showed elevational preferences, and that for at least some species these preferences are reflected elsewhere in their range. The number of species displaying a midelevation distribution in the RS d'Anjanaharibe-Sud (Fig. 8-6D) was low compared with those limited to lowland parts of the forest (Fig. 8-6A), so if this pattern is repeated with further work in other eastern rain forests, the pattern of greater diversity at low elevations (below 1000 m) shown here might be reinforced. A more particular need is for studies of diversity and density at elevations below 800 m. Little forest remains below this elevation in Madagascar (Green & Sussman, 1990; Nelson & Horning, 1993), and what little exists has been poorly studied.

The change in bird density with elevation in the RS d'Anjanaharibe-Sud reflected to some extent the decrease in canopy height with elevation. Canopy height is often related to overall forest foliage complexity (Cody, 1985), and the latter is related to the amount of foraging substrate available for insectivorous birds. However, bird density at 875 m was lower than that at either 1260 or 1550 m (Fig. 8-5B), whereas canopy height was higher at 875 m than at higher elevational zones. This midelevation bulge in density reflects the midelevation bulge in species richness reported by Rahbek (1995) for many different taxa. Rosenzweig

(1992) and Rosenzweig and Abramsky (1993) suggest that the cause of the bulge is that species richness has a nonlinear relationship to productivity and that species richness is highest at middle levels of productivity.

Mixed-Species Flocking Behavior of Forest Birds

The tendency for tropical forest birds to join and follow mixed-species flocks when they are foraging is a widespread and well known phenomenon already documented in Madagascar (Langrand, 1990; Eguchi et al., 1993). This behavior was found here to be a regular feature strongly affecting the distribution pattern of the foraging birds censused along forest trails.

On average over the complete day, about nine foraging birds per hour were seen within 20 m on either side of the footpaths, roughly half of them being associated with mixed flocks (Table 8-13). The flock size was highly variable (range, four to 56 birds of two to 23 species, see Table 8-13) and was probably often underestimated. There was no significant difference in mean flock size or overall number of foraging birds recorded per hour between the two elevational zones surveyed (Table 8-13). Conversely, the number of mixed flocks encountered per hour was significantly depressed at the upper elevation zone, and the overall proportion of foraging birds associated with such flocks (versus foraging alone or in pairs) was also markedly lower at the higher elevational zone.

This suggests that the birds in the lower zone had a stronger tendency to forage in flocks than those in the higher zone. This trend may be re-

TABLE 8-14. Mixed-species flock composition (proportion of all observed flocks in which each species was sighted at two altitudinal levels, and comparative group size in and outside of flocks at the two levels pooled).

Species	% Occurrence in flocks		Mean group size		
	750–950 m	1150–1350 m	In flocks	Outside of flocks	p
Cuculus rochii		7.7	1.0	1.0	NS*
Coua caerulea	7.7	15.4	1.3	1.1	NS
Leptosomus discolor		7.7	1.0	1.0	NS
Philepitta castanea	15.4	23.1	1.9	1.0	†
Neodrepanis coruscans		7.7	2.0	1.3	‡
Coracina cinerea	38.5	30.8	1.9	1.2	‡
Phyllastrephus zosterops	7.7	7.7	2.0	1.5	†
Phyllastrephus madagascariensis	11.5	7.7	1.8	1.5	‡
Phyllastrephus cinereiceps		23.1	2.0	1.4	‡
Hypsipetes madagascariensis	38.5	46.2	1.9	2.0	NS
Pseudocossyphus sharpei		15.4	1.0	1.0	NS
Nesillas typica		15.4	1.0	1.3	NS
Newtonia amphichroa	3.8	23.1	1.3	1.2	NS
Newtonia brunneicauda	84.6	69.2	2.9	1.5	†
Neomixis spp.	50.0	69.2	3.3	1.5	†
Hartertula flavoviridis		15.4	3.0	1.8	‡
Cryptosylvicola randrianasoloi		15.4	2.5	1.6	‡
Pseudobias wardi		15.4	1.5	1.4	NS
Terpsiphone mutata	38.5	46.2	1.8	1.2	†
Zosterops maderaspatana	88.5	76.9	4.1	2.2	†
Nectarinia notata	7.7		1.5	1.5	NS
Nectarinia souimanga	30.8	53.9	1.9	1.3	†
Schetba rufa	3.8		1.0	1.7	NS
Calicalicus madagascariensis	30.8	38.5	1.9	1.3	†
Leptopterus viridis	19.2	23.1	1.6	1.0	NS
Leptopterus chabert	3.8		2.0	2.0	NS
Cyanolanius madagascarinus	38.5	30.8	2.0	1.3	‡
Oriolia bernieri	3.8		2.0		
Hypositta corallirostris	7.7	15.4	2.0		
Tylas eduardi	7.7	30.8	2.2	1.0	†
Dicrurus forficatus	61.5	53.9	2.1	1.6	†
Ploceus nelicourvi	11.5	30.8	1.9	1.0	NS

* NS = nonsignificant (t test).
† p = 0.01 (t test).
‡ p = 0.05 (t test).

lated to forest structure or prey distribution patterns, both of which affect the foraging behavior of birds and thus their ability to remain in flocks. Another factor may be the decreasing number of raptor species from the lower to the upper zone. Two of the four bird predators disappear in the upper zone (*Eutriorchis astur* and *Accipiter henstii*), and the two most abundant raptors (*Buteo brachypterus* and *A. madagascariensis*) were significantly less abundant in the upper than in the lower zone. However, the frequency of occurrence of most widespread flock member species was about as high at both levels (Table 8-14).

Most species also foraged solitarily or more often in pairs or family groups than in flocks (Table 8-14). Only *Zosterops* regularly occurred in monospecific groups of at least three to six birds. The mean group size of individual species, however, was always at least as high in flocks than out of flocks, and in 17 of 32 species, it was significantly higher inside mixed flocks (Table 8-14).

Bird species did not participate equally in mixed flocks, and the mixed-flock members belonged mostly to well-defined guilds (Table 8-11):

1. The terrestrial guild was almost always absent from flocks, and only a few representatives of the small passerines foraging low above the ground (e.g., *Pseudocossyphus* and *Nesillas*) were seen moving with mixed flocks.

2. The frugivorous or nectarivorous species were marginal and occasional members of the mixed flocks: only 21% of all foraging individuals

of this guild recorded were in flocks, although they were among the most active and conspicuous members of the bird community (e.g., *Hypsipetes* and *Nectarinia* spp.).

3. The slow searchers were regular, but still not the most frequent, attendants of the mixed flocks. Some species were never seen in flocks (*Coua reynaudii*, *Brachypteracias leptosomus*, and *Copsychus*), whereas the most active species were among the most typical flock members (*Coracina*, *Terpsiphone*, *Tylas*, and *Dicrurus*). Together, 47.8% of all individuals of this guild were seen associated with a mixed flock.

4. Finally, active gleaners were the main component of foraging flocks. Altogether, 57.6% of individuals belonging to this category were recorded in flocks, making up more than two-thirds of all flock members (Table 8-11). The two rarest species (*Oriolia* and *Hypositta*) were only seen (once each) foraging in flocks.

The mixed-species flocks of this humid forest had a composition and behavior quite similar to those described in another Malagasy humid forest (Eguchi et al., 1993). Their main characteristics and patterns of organization may be summarized as follows:

1. These flocks appeared to be opportunistic groupings of actively foraging birds. Almost every species of the local forest bird community may, at least occasionally, participate in such flocks, and all active searchers, i.e., small or medium-sized arboreal insectivores, were regular attendants in proportions roughly similar to their overall relative abundance.

2. Mixed flocks were most prominent mainly, and sometimes only, in the morning and early afternoon (between 06:00 and 15:00) and during sunny weather. In general, birds showed little activity in the afternoon, especially when the weather was cloudy, and, as a result, were unlikely to form foraging flocks. This follows a general pattern of activity among forest birds.

3. There was not a clear distinction between canopy and understory flocks, most flocks being composed of upper level forest species, occasionally followed by some low understory species foraging below them.

4. The size and species composition of flocks were highly variable, both in space and time, and birds were often seen joining or leaving the flocks.

5. There was not a single species strictly associated with mixed flocks for foraging (obligate follower). All flocking species were seen regularly

foraging alone or in pairs. Even among the most regular flock members, very few species occurred in more than half the flocks surveyed, and only two of them (*Newtonia brunneicauda* and *Zosterops maderaspatana*) were recorded in up to 80% of the flocks.

6. There was no obvious and constant leader species, although the most numerous (*Z. maderaspatana*), noisy (*Hypsipetes madagascariensis*), conspicuous (*Terpsiphone mutata*), or both vocal and demonstrative species (*Dicrurus forficatus*) may play specific roles in flocks.

An original result of this study is the significant (37.8%) decrease (Tables 8-10, 8-13) in the proportion of foraging birds associated with mixed flocks from 875 to 1260 m. At the same time, the number of raptor species that are bird predator specialists (*Accipiter henstii* and *Accipiter madagascariensis*) decreased from two to one, and their mean density decreased from 2 to 1.3 pairs/10 km², whereas the number of other forest raptors species (*Aviceda madagascariensis*, *Eutriorchis astur*, *Polyboroides radiatus*, *Accipiter francesii*, *Buteo brachypterus*, and *Falco zoniventris*) decreased from six to two, and their density decreased from 6.7 to 4.4 pairs/10 km² (Table 9-2, Chapter 9), a decline similar to that of the flocking tendency of insectivorous birds.

Selected Species Accounts

The following annotated list includes data such as breeding information, foraging behavior, display, and calls for (selected) species for which these data are sparse or lacking (Langrand, 1990). Detailed information on the diurnal raptors is presented in Chapter 9.

Madagascar Crested Ibis *Lophotibis cristata*

Song was noted on several evenings at 875 m and 1260 m; displaying birds flew low over the canopy, calling, just after dusk. Also seen foraging on the ground at 850 m.

France's Sparrowhawk *Accipiter francesii*

On 30 November, at 875 m, on adult male *Accipiter francesii* was found dead along a trail. The animal was very fresh, and wounds to the skull

and breast indicated that it had probably been killed by another bird of prey. The stomach and crop of the dead bird contained the remains of five lizards, including complete specimens of a *Zonosaurus*, *Phelsuma guttata*, and *P. lineata* and the tails of single *P. guttata* and *P. lineata*.

Brown Mesite   *Mesitornis unicolor*

At least two groups were found in areas of dense vegetation on slopes at 875 m; both consisted of two individuals.

Madagascar Turtle Dove   *Streptopelia picturata*

A nest with a brooding adult under a large epiphytic fern (*Microsorium punctatum*) was found 3 m up a tree on the edge of a clearing, 1300 m, on 3 November.

Madagascar Blue Pigeon   *Alectroenas madagascariensis*

This species was seen building nests, mostly in low, dense bushes, on 19 October (875 m) and 4 November (1250 m); birds brooding were noted on 30 October (1250 m) and 7 November (1250 m). At 875 m this species was observed feeding on the fruits of *Ephippiandra* (Monimiaceae), which are reddish yellow.

Greater Vasa Parrot   *Coracopsis vasa*

This species was noted regularly in the RNI de Marojejy (Safford & Duckworth, 1990) between August and October 1988. In the RS d'Anjanaharibe-Sud, a few *Coracopsis vasa* were detected by call, and it is probable that more were heard but not identified. However, the great majority of parrot calls and sightings were of *C. nigra*.

Lesser Vasa Parrot   *Coracopsis nigra*

There are a few observations on the diet of this species. At 875 m this species was observed feeding on the ripe reddish yellow fruits of a *Ficus*

(Moraceae), on fruits of *Allophylus* (Sapindaceae), and on the flowers of *Diospyros* (Ebenaceae).

Red-fronted Coua   *Coua reynaudii*

On 5 November at about 900 m, an adult *Coua reynaudii* caught a 5 cm beetle larva and a 7 cm centipede and fed these to young in a nest built below a fallen tree. The nest was less than 1 m above the ground and covered in a net of roots and scrambling bamboo.

Blue Coua   *Coua caerulea*

Several pairs were seen building nests from 19 October at 875 m; one nest was a clump of sticks in a dense bush 4.5 m off the ground. Another nest found on 22 October at 875 m contained one juvenile, which was fed a large homopteran by an adult.

Madagascar Red Owl   *Tyto soumagnei*

Tyto soumagnei was previously recorded at Antanamangotroka, not far from the RS d'Anjanaharibe-Sud (Halleux & Goodman, 1994). In late June 1994 a second individual of this species was captured near Antsahamifelana, along the southwestern limit of the reserve at approximately 14°47'S, 49°28'E and 1000 m elevation. Before the animal was released, it regurgitated a pellet that contained the remains of *Rattus rattus* and *Microgale dryas* (see p. 158, Chapter 10).

African Black Swift   *Apus barbatus*

On 20 November, during the day, this species was seen entering rock holes at about 1800 m.

Madagascar Pygmy Kingfisher   *Ispidina madagascariensis*

At 875 m, on 22 October at 05:00, a single bird was calling loudly (a repeated single "chick") from the tops of 10-m-high trees on a ridgetop. The bird called from the top of about five trees in a radius of 100 m over a 20 min period.

Broad-billed Roller   *Eurystomus glaucurus*

On 20 October, at 875 m, a pair displayed, mated, and entered a tree hole in a large (25-m-tall) isolated tree in a clearing.

Short-legged Ground-roller   *Brachypteracias leptosomus*

About four pairs were present within 2 km of the 875 m camp, and at least three pairs were found at 1250 m in tall valley-bottom forest. Observations of foraging method and food in the RS d'Anjanaharibe-Sud are published in Hawkins (1995). The records of this species at 1250 m are the highest well-documented observations save those of Rand (1936), which may not be accurate (see p. 94). On 29 October and 11 November, one adult fed another adult with a small prey item in what appeared to be courtship feeding.

Scaly Ground-roller   *Brachypteracias squamiger*

At least two pairs were present within 1 km of the 875 m camp.

Pitta-like Ground-roller   *Atelornis pittoides*

This species was only heard calling once at 1150 m, on 3 November. It occurs sympatrically with two other species of ground-roller in (from north to south) the RNI de Marojejy (Safford & Duckworth, 1990), the Masoala Peninsula (where it is rare; Thorstrom & Watson, 1994), PN de Mantadia (Hawkins, pers. obs.), PN de Ranomafana (where it is common; Zack, pers. comm.), and the RNI d'Andringitra (Goodman & Putnam, 1996). Its known elevational range is 0–2000 m (Langrand, 1990). Its rarity in the RS d'Anjanaharibe-Sud is therefore surprising.

Rufous-headed Ground-roller   *Atelornis crossleyi*

On 5 November, at 1230 m, an adult ate a small cockroach. Shortly before dawn on 7 November, at least four and possibly five *Atelornis crossleyi* were calling within a radius of about 50 m, in a damp valley at about 1250 m elevation. After call-

ing for about 5 min, the birds all moved away in different directions; two birds moved away about 80 m and kept calling for at least 10 min afterward. Most birds called from perches 1–2 m from the ground, but one of the five birds calling was perched about 10 m off the ground.

One bird of an apparently adult pair seen at 1950 m was notably duller than the other; only the brighter individual was observed singing. Between 06:00 and 16:30 on 27 November, the duller bird of this pair had moved about 200 m down a river valley.

On 24 November, at 1950 m, an adult walked along a fallen horizontal tree branch and flew up about 1 m from the end of the branch and successfully sally-gleaned an insect (probably a cockroach) from a branch about 1 m away. It then flew 2 m, landed, and ate the insect. This foraging technique has not been described for this species (Turner, 1984; Langrand, 1990) but is used by *Brachypteracias leptosomus* (Hawkins, 1995).

Cuckoo-roller   *Leptosomus discolor*

On 4 November, at 875 m, an adult flew across a valley holding a large cricket in its bill, presumably to feed young.

Velvet Asity   *Philepitta castanea*

At 875 m an adult male in breeding plumage was observed eating small red berries from an understory shrub of *Psychotria* (Rubiaceae). A female plumage bird was observed at 1260 m feeding on the yellow fruits of a species of Lamiaceae; the bird seemed to be preferentially avoiding unripe green fruits. In the 1550 m zone, this species was noted consuming the fruits of *Canthium* (Rubiaceae).

Sunbird-asity   *Neodrepanis coruscans*

On 2 November, at 1250 m, a nest was located 8 m up in a hanging vine near a clearing. It was attended by a male that brought small unidentified insects to unfledged young. At 1260 m this species was observed visiting the flowers of *Gaertnera* (Rubiaceae) and *Mimulopsis* (Acanthaceae). The latter plant was also being simultaneously exploited by *Nectarinia souimanga*.

Yellow-bellied Sunbird-asity   *Neodrepanis hypoxantha*

Newly fledged juveniles were seen on 14 November at 1600 m, on 27 November at 1950 m, and on 2 December at 2010 m. They were dull olive green above with unmarked yellow underparts, somewhat duller than the adults, with olive green-tinged flanks. The bills were almost straight and had conspicuous pale pink mandible bases. Near the summit of the RS d'Anjanaharibe-Sud, adults were frequently seen on sunny days flycatching from the tops of low shrubs.

At 1550 m this species was observed visiting the flowers of *Bakerella* (Loranthaceae) and a Lamiaceae. In the former case, the same cluster of flowers was also frequented by *Nectarinia souimanga*.

Ashy Cuckoo-shrike   *Coracina cinerea*

In late October, at 875 m, an adult was constructing a cup-shaped nest on a horizontal branch 6 m from the ground in an isolated tree in a clearing. Adults were seen feeding newly fledged juveniles on 19 October at 875 m, on 10 November at 1250 m, and on 15 November at 1600 m.

Spectacled Greenbul   *Phyllastrephus zosterops*

A single *Phyllastrephus zosterops* was observed sitting on a cup-shaped nest on 19 October at 875 m. The nest was suspended between the bases of two narrow horizontal branches of a low shrub, 2 m from the ground. An adult was feeding two newly fledged juveniles on 8 November at 900 m. Food items included a green bush cricket.

Grey-crowned Greenbul   *Phyllastrephus cinereiceps*

This species was common in both the 1250 m and 1550 m elevational zones. It was not detected frequently on point counts because its call is rather weak, but individuals were seen in about 10 different locations in these zones.

A nest was found on 9 November at 1240 m. It was a deep cup (5–7 cm) hanging from the base of a lower fork of a 1.5 m high shrub. The neat nest cup was about 1 m from the ground, made of moss, and lined with dry grass and palm fibers.

It contained two young nestlings. At least three adults were attending the nest and mobbed the observer. On 12 November at 1250 m, a different group of four was accompanied by a recently fledged juvenile.

Madagascar Bulbul   *Hypsipetes madagascariensis*

At 700 m, on 10 November, an adult was feeding two juveniles in a cup-shaped nest placed at the end of a branch 4 m above the main road. Two adults were feeding a newly fledged juvenile at 1550 m on 17 November. At 875 m this species was observed feeding on the fruits of *Canthium* (Rubiaceae) and *Dianella ensiofolia* (Liliaceae).

Madagascar Magpie-robin   *Copsychus albospecularis*

A male was feeding young in a tree-hole nest at 1260 m on 5 November.

Forest Rock-thrush   *Pseudocossyphus sharpei*

Adults were feeding fledglings on 4 November at 1250 m. Many nests of this species were found at 1260 and 1550 m, including one at 1260 m built in the wall of an abandoned shelter. This same nest contained two nestlings and one egg on 4 November, three nestlings on 7 November, and one nestling on 12 November. On 9 November at 1260 m, another nest at 1250 m was found hidden under a protruding root, 30 cm above the ground. An adult was feeding a newly fledged juvenile at 1950 m on 28 November.

Madagascar Brush-warbler   *Nesillas typica*

A recent fledgling seen at 1250 m on 8 November was dull gray-brown all over, and had a short tail. An adult was feeding a newly fledged juvenile on 25 November at 1950 m.

Brown Emutail   *Dromaeocercus brunneus*

An adult was feeding a newly fledged juvenile at 1950 m on 2 December. The juvenile was even darker rufous brown than the adult, lacked the

characteristic gray ear coverts of the adult, and had a shorter bill, an orange gape, and a shorter, fully barbed tail.

Rand's Warbler   *Randia pseudozosterops*

Randia pseudozosterops was recorded rarely on point counts. However, at 1250 m it was relatively frequently encountered in mixed-species flocks. On 7 November at 1230 m, two adults were seen with two recent fledglings in a mixed-species flock. The juveniles were similar in plumage to the adults but gave a series of loud, high hissing notes.

Red-tailed Newtonia   *Newtonia fanovanae*

This species was rediscovered in 1989 and has been recorded in lowland forest near Maroantsetra and on the Masoala Peninsula (Langrand & Sinclair, 1994; Goodman, 1995), in the RS d'Ambatovaky (Thompson & Evans, 1991), and around the RNI d'Andohahela (Goodman & Schulenberg, 1991; Goodman et al., 1997). In the RS d'Anjanaharibe-Sud, it was seen once in a mixed-species flock at 950 m elevation in rather degraded forest, near the village of Andranotsarabe, and one was heard singing in a mixed-species flock in the 875 m elevational zone.

Cryptic Warbler   *Cryptosylvicola randrianasoloi*

A group of *Cryptosylvicola randrianasoloi* consisting of three adults and at least two juveniles was noted at 1550 m on 22 November. The juveniles were dark, dull green-gray on the back and head, slightly greener on the mantle, and browner on the wings. The head lacked the conspicuous supercilium and eye stripe of the adult. The underparts were dull, pale gray and slightly mottled on the breast but showed no trace of the adult's yellow throat pattern. The bill was all dark, with a conspicuous pale orange gape, and the feet and legs were dark horn.

Ward's Flycatcher   *Pseudobias wardi*

Pseudobias wardi was common in mixed-species flocks and at the edge of forest. Several pairs appeared to be holding territories in tall trees on the edge of clearings at 875 m and 1250 m. This species appeared to be highly territorial. On 14 November at 1300 m, a dispute between at least six individuals was noted. The interaction lasted about 20 sec, and individuals, while calling loudly, flew at each other and made contact in mid-air. After the dispute, three pairs flew off in different directions.

Crossley's Babbler   *Mystacornis crossleyi*

On 25 October, at 875 m, an adult male was feeding a single, mostly downy, young perched at 10 cm above the ground on roots at the base of a *Pandanus* sp. The young was chocolate brown on the head and back and paler orange-brown on the breast with a whiter belly. The gape was orange, and the legs were grayish.

Madagascar White-eye   *Zosterops maderaspatana*

A flock of *Zosterops* was observed at 875 m feeding on the flower buds of *Medinilla* (Melastomataceae).

Hook-billed Vanga   *Vanga curvirostris*

On 26 October, at 875 m, a *Vanga curvirostris* caught a 5-cm *Phelsuma* and ate it whole.

White-headed Vanga   *Leptopterus viridis*

On 12 November at 1250 m, a male *Leptopterus viridis* gave a late-instar brown cricket to a recently fledged juvenile. An adult male, accompanied by a food-begging juvenile, ate a 5 cm *Calumma nasuta* at 1250 m on 2 December.

Chabert's Vanga   *Leptopterus chabert*

On 22 October at 875 m, a pair of *Leptopterus chabert* was attending a cup-shaped nest constructed on top of a 10-cm-wide horizontal tree branch, 7 m up in a lone tree in a *tavy* clearing. Other pairs were observed incubating or feeding young in isolated trees in the middle of *tavy* clearings at 900 m on 20 and 29 October.

Blue Vanga *Cyanolanius madagascarinus*

A *Cyanolanius madagascarinus* was construct-ing a nest in a tree on 5 November at 1250 m.

Bernier's Vanga *Oriolia bernieri*

Only one *Oriolia* was seen, at 900 m on 28 October. In the RNI de Marojejy, this species was sparsely distributed, being common at a 900 m study site and absent from four other sites be-tween 300 and 1600 m (Safford & Duckworth, 1990).

Helmet Vanga *Euryceros prevostii*

Euryceros was fairly common at 875 m (about four different pairs or families observed within 1 km of camp). This species was recorded only once at 1250 m, which appears to be at the upper limit of its elevational distribution (Langrand, 1990).

Nuthatch Vanga *Hypositta corallirostris*

At 875 m a nest of *Hypositta* was found 6 m up in a 40 cm dbh tree. The nest was placed against the trunk, in a small surface fissure, below which was a slight scar forming a bulge. The nest was made of tree-fern fibers formed into a 4–5 cm deep cup and lined with a few dead leaves. The nest was visited by adults on 26 October but empty and apparently abandoned on 27 October when checked by observers. This appears to be the first description of this species' nest.

Tylas Vanga *Tylas eduardi*

On 10 November, at about 700 m, an adult *Ty-las* was feeding a recent fledgling in a mixed-spe-cies flock. A group of three *Tylas* at 1250 m on 2 December contained an apparently adult bird with a white chin and throat. This color pattern is also known from the western race, *Tylas eduardi albigularis*, not previously recorded from rain for-est and scarce in the west (Langrand, 1990; Haw-kins, 1994), and from female *T. eduardi* in RS d'Ambohitantely (Langrand, pers. comm.). The white-throated individual had a bright orange breast and belly, unlike most individuals of *T. e.*

albigularis, which are pale orange or whitish be-low. The same group contained a food-begging juvenile, which had a black chin and throat.

Crested Drongo *Dicrurus forficatus*

Two nests found on 6 and 8 November at 1250 m both contained unfledged young (two in one nest) and were built in the tops of isolated trees in clearings. One adult brought a 3 cm beetle to feed young. Another two nests were found on 12 November at about 900 m.

Nelicourvi Weaver *Ploceus nelicourvi*

A female *Ploceus nelicourvi* was observed feeding a newly fledged juvenile on 4 November. The juvenile was green on the head and back, grayish underneath and had a pale yellow bill.

Conclusions

The RS d'Anjanaharibe-Sud holds an extremely high proportion of the resident forest bird species that would be expected to occur in humid forest. For several species, notably *Atelornis crossleyi* and *Neodrepanis hypoxantha*, population densi-ties are high. Other endemic species, e.g., *Eutrior-chis astur* and *Newtonia fanovanae*, are restricted in distribution, and their presence in the RS d'Anjanaharibe-Sud is of considerable conserva-tion importance.

The bird community of the RS d'Anjanaharibe-Sud changed considerably with elevation. The number of forest bird species declined more or less linearly from 70 at 875 m to 25 at 1950 m. However, forest bird density was highest at 1250 m, lower at 1550 m, and lower still at the most species-rich camp at 875 m. Density was lowest at 1950 m.

The majority of species (52 of 60, or 87%) for which an interpretable sample size was gathered showed elevationally limited distributions. Thirty did not occur regularly at or above 1550 m, and eight did not occur regularly below 1250 m. Only two species (*Neodrepanis hypoxantha* and *Saxi-cola torquata*) occurred only at or above 1550 m. Nine species occurred only in the lowest zone (875 m). At a coarse level, the forest bird com-munity can be divided into two groups, species

that are most common below and those that are most common above 1000–1200 m. There was little evidence of species replacement with elevation; it was suspected in only three cases, only one of which concerned two congeneric species (*Neodrepanis*).

Variation of bird communities with habitat type within elevational zones was not well marked. Vegetation structure measures showed that within-elevational zone variation was characterized by a tendency to low canopy and dense understory on ridges compared with valleys. However, this variation could not be used to account for much variation in the bird community.

Of the survey methods used, point counts (five repeated samples at the same point) were time consuming; however, they provided a great deal of new information about species density that in some cases did not agree with detection rate information about the same species. It is presumed that the density figures calculated using point-count data are the more reliable of the two because they depend on fewer unsupported assumptions.

Five repeated point-count samples produced about 50% data redundancy at all elevational zones. Species-accumulation curves suggest that even after five repeated samples at a point-count site there is a high proportion of species that remain undetected. This may be due to forest bird species moving between point-count sample sites over the period of sampling. If sample points are not limited (e.g., to where an extensive trail network is available), then limiting the repeated samples to one or two will increase greatly the efficiency and representativeness of sampling. Active searching was the best method for compilation of inventory information, and call playback proved almost ineffectual.

Acknowledgments

Literature Cited

BENSON, C. W., J. F. R. COLEBROOK-ROBJENT, AND A. WILLIAMS. 1977. Contribution à l'ornithologie de Madagascar. L'Oiseau et Revue Française d'Ornithologie, **47:** 41–61.

BIBBY, C. J., N. D. BURGESS, AND D. A. HILL. 1992. Bird Census Techniques. Academic Press, London, xv + 257 pp.

BUCKLAND, S. T., D. R. ANDERSON, K. P. BURNHAM, AND J. L. LAAKE. 1993. Distance Sampling: Estimation of Abundance of Biological Populations. Chapman and Hall, London, xii + 446 pp.

CARLETON, M. D., AND D. F. SCHMIDT. 1990. Systematic studies of Madagascar's endemic rodents (Muroidea: Nesomyinae): An annotated gazetteer of collecting localities of known forms. American Museum Novitates, **2987:** 1–36.

CODY, M. L. 1985. An introduction to habitat selection in birds, pp. 3–56. *In* Cody, M. L., ed., Habitat Selection in Birds. Academic Press, Orlando, Fla, xvi + 558 pp.

EGUCHI, K., S. YAMAGISHI, AND V. RANDRIANASOLO. 1993. The composition and foraging behaviour of mixed-species flocks of forest-living birds in Madagascar. Ibis, **134:** 91–96.

GOODMAN, S. M. 1995. The third known specimen of the Red-tailed Newtonia *Newtonia fanovanae* (Family Sylviidae), a Malagasy endemic. Bulletin of the British Ornithologists' Club, **115:** 130–132.

GOODMAN, S. M., A. ANDRIANARIMISA, L. E. OLSON, AND V. SOARIMALALA. 1996. Patterns of elevational distribution of birds and small mammals in the humid forests of Montagne d'Ambre, Madagascar. Ecotropica, **2:** 87–98.

GOODMAN, S. M., M. PIDGEON, A. F. A. HAWKINS, AND T. S. SCHULENBERG. 1997. The birds of southeastern Madagascar. Fieldiana: Zoology, n.s., **87:** 1–132.

GOODMAN, S. M., AND M. S. PUTNAM. 1996. The birds of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar, pp. 171–190. *In* Goodman, S. M., ed., A floral and faunal inventory of the eastern slopes of the Réserve Naturelle d'Andringitra, Madagascar: With reference to elevational variation. Fieldiana: Zoology, n.s., **85:** 1–319.

GOODMAN, S. M., AND T. S. SCHULENBERG. 1991. The rediscovery of the Red-tailed Newtonia *Newtonia fanovanae* in south-eastern Madagascar with notes on the natural history of the genus *Newtonia*. Bird Conservational International, **1:** 33–45.

GREEN, G. M., AND R. W. SUSSMAN. 1990. Deforestation history of the eastern rain forests of Madagascar from satellite images. Science, **248:** 213–215.

HALLEUX, D., AND S. M. GOODMAN. 1994. The rediscovery of the Madagascar Red Owl *Tyto soumagnei* (Grandidier 1878) in north-eastern Madagascar. Bird Conservation International, **4:** 305–311.

HAWKINS, A. F. A. 1994. Conservation status and regional population estimates of the White-breasted Mesite *Mesitornis variegata*, a rare Malagasy endemic. Bird Conservation International, **4:** 279–303.

———. 1995. Foraging observations on a Short-legged Ground-roller *Brachypteracias leptosomus*. Newslet-

ter of the Working Group on Birds in the Madagascar Region, **5**(2): 11–13.

LAAKE, J. L., S. T. BUCKLAND, D. R. ANDERSON, AND K. P. BURNHAM. 1993. DISTANCE User's Guide V2.0. Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, Colo.

LANGRAND, O. 1990. Guide to the Birds of Madagascar. Yale University Press, New Haven, Conn., xi + 364 pp.

LANGRAND, O. 1995. Guide des Oiseaux de Madagascar. Delachaux et Niestlé editions, Lausanne et Paris.

LANGRAND, O., AND J. C. SINCLAIR. 1994. Additions and supplements to the Madagascar avifauna. Ostrich, **65**: 302–310.

NELSON, R., AND N. HORNING. 1993. AVHRR-LAC estimates of forest area in Madagascar, 1990. International Journal of Remote Sensing, **14**: 1463–1475.

NICOLL, M. E., AND O. LANGRAND. 1989. Madagascar: Revue de la Conservation et des Aires Protégées. World Wide Fund for Nature, Gland, Switzerland, xvii + 374 pp.

POWZYK, J. 1995. Sighting of Madagascar Red Owl (*Tyto soumagnei*) in Mantadia National Park. Newsletter of the Working Group on Birds in the Madagascar Region, **5**(2): 5.

RAHBEK, C. 1995. The elevational gradient of species richness: A uniform pattern? Ecography, **18**: 200–205.

RAND, A. L. 1932. Mission Franco-Anglo-Américaine à Madagascar: Notes de voyage. L'Oiseau et la Revue Française d'Ornithologie (nouvelle série), **2**: 227–282.

———. 1936. The distribution and habits of Madagascar birds: A summary of the field notes of the Mission Zoologique Franco-Anglo-Américaine à Madagascar. Bulletin of the American Museum of Natural History, **72**: 143–499.

RANDRIAMANINDRY, J.-J. 1995. The Dusky Greenbul *Phyllastrephus tenebrosus* in Zahamena Strict Reserve, Madagascar. Newsletter of the Working Group on Birds in the Madagascar Region, **5**(1): 1.

RECHER, H. F. 1981. Report of working group on the need for standardized census methods. Studies in Avian Biology, **6**: 580–581.

REYNOLDS, R. T., J. M. SCOTT, AND R. A. NUSSBAUM. 1980. A variable circular-plot method for estimating bird numbers. Condor, **82**: 309–313.

ROSENZWEIG, M. L. 1992. Species diversity gradients: We know more and less than we thought. Journal of Mammalogy, **73**: 715–730.

ROSENZWEIG, M. L., AND Z. ABRAMSKY. 1993. How are diversity and productivity related? pp. 52–65. *In* Ricklefs, R., and D. Schluter, eds., Species Diversity in Ecological Communities: Historical and Geographical Perspectives. University of Chicago Press, Chicago, 414 pp.

SAFFORD, R. J., AND J. W. DUCKWORTH, EDS. 1990. A wildlife survey of Marojejy Reserve, Madagascar. ICBP Study Report 40. International Council for Bird Preservation, Cambridge, 172 pp.

SALOMONSEN, F. 1934a. On a hitherto unknown fauna of montane birds in central Madagascar. Novitates Zoologicae, **39**: 207–215.

———. 1934b. Remarks on the montane avifauna in central Madagascar. Bulletin of the British Ornithologists' Club, **54**: 9–12.

TERBORGH, J. 1977. Bird species diversity on an Andean elevational gradient. Ecology, **58**: 1007–1019.

THOMPSON, P. M., ED. 1987. Zahamena Forest (Madagascar) Expedition 1985. ICBP Study Report 20. International Council for Bird Preservation, Cambridge.

THOMPSON P. M., AND M. I. EVANS, EDS. 1991. A survey of Ambatovaky Special Reserve, Madagascar. Madagascar Environmental Research Group, London.

THORSTROM, R., AND R. T. WATSON. 1994. Avian inventory of Masoala Peninsula, Madagascar. The Peregrine Fund, Boise, Idaho.

TURNER, D. A. 1984. The ground-rollers of Madagascar, pp. 553–557. Proceedings of the 5th Pan-African Ornithological Congress. Southern African Ornithological Society, Johannesburg.

Chapter 9

The Diurnal Raptors (Falconiformes) of the Réserve Spéciale d'Anjanaharibe-Sud: Abundance, Distribution, and Conservation

Jean-Marc Thiollay[1]

Abstract

All diurnal raptors were searched intensively within two 30 and 25 km^2 study areas at 750–950 m and 1000–1400 m, respectively, in the mostly forested range of the Réserve Spéciale d'Anjanaharibe-Sud. Density estimates were obtained by mapping the location movements and behaviors of all individual birds detected from understory and openings.

Habitat selection, distribution, abundance, and behavior of the 10 resident species are given, including a sighting of the threatened Madagascar Serpent Eagle, *Eutriorchis astur*. The reliance of several species on the little remaining nondisturbed natural forest and the implications of this are stressed.

Résumé

Tous les rapaces diurnes furent recherchés systématiquement sur deux zones d'étude de 30 et 25 km^2, respectivement entre 750 et 950 m pour la première et 1000–1400 m pour la seconde dans la réserve boisée d'Anjanaharibe-Sud. Des estimations de densité furent obtenues pour chaque espèce en cartographiant les observations de tous les individus détectés, leurs mouvements et leurs comportements.

Le choix de l'habitat, la distribution et les modes de chasse des espèces résidentes sont détaillés, y compris une observation de l'Aigle-autour de Madagascar, *Eutriorchis astur*. L'association étroite de plusieurs espèces avec la grande forêt peu ou pas perturbée est soulignée, ainsi que les implications pour leur conservation.

Introduction

Being top predators and among the largest species, birds of prey often have relatively low densities, large home ranges, low reproductive rates, and specialized food requirements. As a result, they are among the most demanding bird species in terms of habitat quality and minimum area required to sustain a viable population. Many species are also highly sensitive to human disturbance and habitat degradation. As usual with habitat and food specialists and widely ranging species, they are often reliable indicators of habitat changes or disturbance, both on landscape and local scales, and therefore they may be used to assess the conservation value of an area (Thiollay, 1994). Because of their distribution patterns, they play the role of "umbrella species." An area encompassing a viable and complete community of raptors is likely to harbor all the representative natural habitats of the region and sizeable popu-

[1] Laboratoire d'Ecologie, Ecole Normale Superieure, 46, Rue d'Ulm, 75230 Cedex 05, France.

lations of most, if not all, other bird species, especially in tropical forests, where many raptors have low densities or uneven distributions (Thiollay, 1989a).

The first goal of this study was to conduct an intensive survey of all raptor species over the largest possible area and the widest elevation range within the Réserve Spéciale (RS) d'Anjanaharibe-Sud, with an emphasis on overall densities, altitudinal distributions, and habitat selection. The ultimate goal of this raptor survey was to assess the conservation state and value of the RS d'Anjanaharibe-Sud through an analysis of its raptor population. However, the time spent at each locality was too short to obtain more than a rough estimate of the minimum population size of each species within a restricted study area, a general pattern of habitat use, and occasional data on breeding, food, and foraging behavior.

Study Areas

A detailed description of climate, vegetation, and fauna along the complete elevational gradient of this survey is given elsewhere in this volume. Here I briefly mention the main features of my two study areas that may be among the most influential for raptors and their community composition.

The lower study area, surveyed from 18 to 31 October 1994, extended mainly between 750 and 950 m (extreme range, 670–1070 m). The moist montane forest cover reached 30 m tall on most lower slopes (rarely up to 40 m) and generally decreased in stature with elevation to 10–15 m tall on the highest ridges. Accordingly, the canopy cover became increasingly less continuous from the lower to upper slopes. The understory remained usually quite open, with a frequent groundcover of dwarf bamboo and locally dense stands of *Pandanus*. Most valley bottoms and gentle lower slopes were cleared for shifting cultivation, particularly below 1000 m, although many of these huge clearings were more or less recently abandoned and overgrown by dense, often monospecific, stands of early successional trees (*Harungana madagascariensis*) that may reach up to 10 m in the oldest clearings. The natural forest was mainly restricted to upper or steeper slopes and narrow ridges.

The upper study area, whose southeast corner was close to the northwestern corner of the lower

quadrat, was surveyed from 1 to 13 November 1994. The elevation ranged mostly between 1000 and 1400 m, but the study area extended down to 900 m along the southern limit and up to almost 2000 m on the western side. The forest remained tall with a relatively open understory on the lower slopes and deep valley bottoms, but became distinctly shorter in stature, especially over 1100–1200 m. On the many narrow ridges and steep upper slopes, the humid montane forest, heavily coated with mosses and epiphytes, was only 2–3 to 5–10 m tall and had a dense undergrowth. Bamboos and tree ferns were more abundant than below. Rocky areas were also more frequent. The markedly decreasing temperatures probably had important consequences, e.g., on the invertebrate fauna, as suggested by the disappearance of leeches. The large *tavys*, i.e., clearcut patches for shifting cultivation, so prominent in the lower area, encroached upon the southern third of the upper area. However, portions of the remaining forest were heavily disturbed by multiple gaps, usually small and recently overgrown by secondary vegetation, that were the result of illegal mining activities.

In both areas, and in addition to large clearings and numerous mining gaps, there was much evidence throughout the study areas, at least along the many footpaths, of regular human disturbance. Many trees were either felled, stripped of bark, or damaged. Significant hunting pressure was also suggested by lemur traps. This diffuse human exploitation of dispersed natural resources may have affected the forest structure, if not its vertebrate community.

Methods

Within each of the two elevational zones, I defined a study area according to existing trails, footpaths, ridges, openings, and dominant lookouts, allowing the most complete survey in every direction during full-day walks. As usual in tropical forests (Thiollay, 1989b), the most efficient technique for locating raptors was to watch flying or soaring birds over the forest from human-made openings or natural gaps, preferably dominant lookouts, during the middle and late sunny morning hours, when many raptors soar and display almost exclusively (Table 9-1). All forest raptors in this community were likely to soar and/or display over the canopy, although some species (*Bu-*

TABLE 9-1. Number of independent records of each raptor species in the lower (750–950 m) and upper (1100–1400 m) study areas and in three different conditions.

	Study area					
	Openings (08–12 hr)		Openings (<08, >12 hr)		Forest understory	
Records	Lower	Upper	Lower	Upper	Lower	Upper
Time spent (hr)	35	18	22	15	95	97
Aviceda madagascariensis		1	1	1	1	2
Eutriorchis astur					2	
Polyboroides radiatus	8		5		2	
Accipiter henstii	4		3		4	
Accipiter madagascariensis	3	2	5	2	3	2
Accipiter francesii	2	2	3	2	4	
Buteo brachypterus	79	45	37	33	40	58
Falco newtoni	42	19	21	12		
Falco zoniventris		1		3		
Total records/hr	3.9	3.9	3.4	3.5	0.6	0.6

teo and *Polyboroides*) did it much more frequently than others (*Aviceda* and *Accipiter*). The breeding season was at its height during the survey for several, if not all, species, and their activity or conspicuousness was presumably optimal.

Systematic daily surveys were planned to cover each study area several times and to stay at the most convenient vantage points during the best hours and weather conditions. I spent 1–4 consecutive morning hours in openings, carefully looking for raptors in all possible directions and at all distances. I recorded the period during which they were visible, their sex, age, and behavior. Flight paths were recorded on a 1:50,000 map, controlled by subsequent Global Positioning System coordinates and using compass, altimeter, and local features. In the forest understory, I walked alone, slowly and silently, carefully searching for perched or flying raptors. The location of every bird sighted, heard calling within 100 m, or seen flying overhead was recorded on an enlarged map of the area. Overall, I spent, outside rainy periods, at least 282 hr in field surveys, 192 of which were in the forest understory.

Each independent record (see Table 9-1) was the sighting of one or more individuals, seen together or simultaneously, from the same point. It also included birds only heard calling within 100 m of the observer. Records were considered different from each other when made more than 100 m and 30 min apart or made more than 1 hr apart if made from the same place.

Assessment of the minimum number of pairs was always based on location of the observed individuals and mapping of their movements, not on the frequency of records, to minimize the potential bias in favor of more conspicuous species. This mapping method on a large quadrat involved individual differentiation to separate records between different pairs, most of them presumed to be breeding, territorial, and using more or less nonoverlapping home ranges. Because no individual marking was possible, I relied heavily on behavior and movement pattern of observed birds, such as nuptial display flights, birds carrying prey over long distances (presumably to nests), and social interactions between neighboring pairs (particularly *Buteo*) to individually identify birds. Nests found and adults followed by still dependent young provided additional clues. The resulting density estimate was the minimum number of resident pairs actually recorded one or more times. For secretive species, the presence of a pair was sometimes inferred from observations of individual adults far from any other sighting. In every case, two adjacent pairs of *Buteo* were considered different from each other only after both pairs were seen simultaneously.

Because of these criteria, and of the inconspicuousness of some species (notably *Aviceda* and *Accipiter* spp.), some pairs may have been missed or seen but not identified as such; consequently, the density estimates are conservative. On the other hand, the home range of some peripheral pairs may have overlapped the arbitrarily drawn limits of the study areas, and this would have led to overestimation of the density. These data must be considered, and are used, only as abundance indices for a comparison between different areas, not as actual densities.

TABLE 9-2. Density estimates (minimum number of pairs) of raptors in two sample study areas.*

| | Elevational zone | | | | | |
| | Lower (750–950 m) | | | Upper (1100–1400 m) | | |
Records	Core area (20 km²)	Marginal area (10 km²)	Overall/ 10 km²	Core area (15 km²)	Marginal area (10 km²)	Overall/10 km²
Aviceda madagascariensis	1 (2)		0.5	1 (2)		0.7
Eutriorchis astur	1		0.5			
Polyboroides radiatus	2	1	1.0	(1)		≤0.7
Accipiter henstii	1 (2)	(1)	≥0.5			
Accipiter madagascariensis	3		1.5	2		1.3
Accipiter francesii	2 (3)		1.0	1	1	0.8
Buteo brachypterus	7	4 (5)	3.7	8 (9)	3	4.4
Falco newtoni	2	1	1.0	2	1	1.2
Falco zoniventris				(1)	1	≤1.0
Total	19 (22)	6 (8)	≥9.7	14 (18)	6	≤10.1

* In some territories the core and marginal subareas overlapped, but to simplify, the corresponding pairs were assigned to one side only. The upper range of the population estimate is given in parentheses. It is derived from inconclusive evidence of additional pairs or from pairs widely ranging outside the limits of the study area. The overall density is calculated on the minimum figure in the subarea(s) where the species were recorded.

Each study area was a polygon, as closely square shaped as possible. Because of varying accessibility to different parts, a distinction was made between a core area searched from both openings and understory and a marginal area, where only vantage points overlooking the forest were used. In the latter area, only the most conspicuous, regularly soaring species were satisfactorily censused (*Buteo* and *Polyboroides*). It must be stressed that all the areas, and hence densities, were calculated from maps using a planimetric scale. In fact, the terrain was so rough, with deep valleys and steep slopes, that the actual area of forest available within a given planimetric patch was probably almost twice as much as that considered for density estimates.

Habitat selection was quantified by the frequency of occurrence of each species in four main habitat categories: little-disturbed tall forest (15–35 m), mostly on lower slopes; short, dense forest (3–14 m), usually on ridges; forest edges, mining gaps, and old, abandoned *tavys*; and large clearings (*tavys*, roads, and settlements). For each independent observation of perched or foraging birds, independent of the number of individuals, I recorded the habitat category. Because of the low number of records for several species and a lack of significant differences between study areas, I combined the data from the two levels. The relative area of each habitat type was visually estimated in the field on each subsquare of a grid-lined map of the study area. Being crude mea-

surements, these estimates were not used for a statistical comparison between the frequency of used versus available habitats. Moreover, the exact time that I spent in each habitat was not recorded and was unevenly distributed between habitats.

Results

Community Structure

The local pool of resident birds of prey included 10 species known to be potentially breeding and regular in forested areas of northeastern Madagascar (Langrand, 1990). Only two of them, *Falco zoniventris* and *F. peregrinus*, were not recorded in the lower study area but were present in the nearby upper area and usually occurred in the lowlands. Among the eight species actually recorded in the lower area, *Eutriorchis astur* was rare, *Aviceda madagascariensis* was patchily distributed, and *Accipiter henstii* had a low density. Four other species had almost similar intermediate abundances (around one pair per 10 km²), although with different distribution patterns and habitat uses: *Polyboroides radiatus, Accipiter madagascariensis, Accipiter francesii*, and *Falco newtoni* (Table 9-2). About one-third of all pairs of raptors identified were *Buteo brachypterus*, by far the dominant species (Table 9-2).

TABLE 9-3. Habitat use of observed perched and/or foraging individuals in upper and lower study areas combined.*

Records (total)	% Occurrence in habitat types			
	Tall forest (slopes)	Short forest (ridges)	Edges, gaps, and disturbed forest	Large clearings and second growth
Relative area, %	30	35	20	15
Aviceda madagascariensis (6)	83		17	
Eutriorchis astur (2)	100			
Polyboroides radiatus (14)	50	21	29	
Accipiter henstii (10)	100			
Accipiter madagascariensis (15)	59	13	21	7
Accipiter francesii (13)	69		31	
Buteo brachypterus (261)	49	29	18	4
Falco newtoni (94)			15	85
Falco zoniventris (4)			100	

* See text for habitat description.

At first sight, the upper study area, as compared with the lower one, was missing only *Eutriorchis astur* and *Accipiter henstii*, although the latter is known to occur elsewhere at such elevation. *Falco zoniventris* was found only in the upper area, and the six other species had roughly the same overall densities in the two areas (Table 9-2). This was, in fact, misleading because four species occurred mainly, if not only, below 1100 m, i.e., within the lower range of the upper zone. These were *Aviceda madagascariensis, Polyboroides radiatus, F. newtoni,* and *F. zoniventris.* Moreover, *F. newtoni* occurred only in open areas, all of which were below 1100 m. Only *Accipiter madagascariensis* and *Buteo brachypterus* regularly occurred in the forest above 1100 m. *Buteo brachypterus* was the dominant species in both upper and lower areas, accounting for more than half of all the resident raptors recorded. Overall, *Accipiter madagascariensis* and *Buteo brachypterus* did not significantly decrease in abundance between 700 and 1500 m.

Species Accounts

Madagascar Cuckoo-Falcon   *Aviceda madagascariensis*

This secretive species was either rare, very local, or too elusive to be detected regularly. Its voice is unknown (Langrand, 1990), but no bird call was heard that could not be attributed to a known raptor or was not reminiscent of the voice of any of the other African or Asian *Aviceda* sp. The seven records were all below 1100 m, except for one sighting by F. Hawkins at about 1400 m, an elevation where it was also recorded in the nearby Réserve Naturelle Intégrale (RNI) de Marojejy (Safford & Duckworth, 1988). All our records were in the forest canopy or along the forest edge near the road (Table 9-3). This species soars easily over the forest (but infrequently) like all other cuckoo-falcons. In flight, it can be distinguished from the superficially similar *Buteo* by its flat wings (not V-shaped); its longer tail, which is not as spread as that of a soaring *Buteo*; its heavily barred underwing feathers; three well-marked tail bands below the whitish rump; and its slender, more protruding head.

Madagascar Serpent Eagle   *Eutriorchis astur*

More than 50 years after the last specimens were collected, this species was recently recorded in the nearby RNI de Marojejy (Safford & Duckworth, 1988) and on the Masoala Peninsula (Thorstrom et al., 1995). This indicates that scattered populations may still exist in the rain forest patches of northeastern Madagascar. However, this species remains decidedly rare or elusive. Despite a careful search, it was seen only on 30 October on the trail demarcating the southeastern limit of the RS d'Anjanaharibe-Sud, first in the morning, then about 200 m farther away in the early afternoon. The first time, one individual flew low over the forest, uttering a rather soft, three-note call that sounded more like the call of a cuckoo than the

call of a raptor. It perched in the canopy in full view about 40 m away but did not allow me to get a closer view, and it disappeared as soon as I approached it. Both when perched and in flight, its long banded tail was prominent, and it had a strongly barred underside. The second sighting was equally brief but at closer range. A bird gliding down at low canopy level snatched an unidentified prey in the foliage in front of me. After struggling with the prey for a few seconds, the raptor flew off, again gliding down in the understory, probably carrying its prey. It was seen only from above. The long, banded tail and the relatively big head were the only characters noticed. This kind of attack was much like the hunting technique of *Buteo brachypterus*, but the bird had definitely darker brown upperparts, wider but relatively shorter wings, and a strikingly long tail that was spread when the bird mantled its prey on the branch. In both cases, the flight was slower, more direct, and with fewer and less rapid wingbeats than the swift flight of *Accipiter henstii*. This bird appeared to be larger than the latter.

These two records, which may relate to the same individual, were made in one of the lowest parts of the reserve, around 700 m, and in one of the tallest, most humid, and undisturbed lowland forest stands surveyed with the highest concentration of really big trees encountered along the whole gradient studied. It may be not coincidental that the only record of this lowland rain forest bird was made in this last remaining patch of seemingly suitable habitat. However, it may also occur in disturbed areas of the Masoala Peninsula (Thorstrom et al., 1995).

Madagascar Harrier-Hawk *Polyboroides radiatus*

I saw this rather conspicuous raptor in the lower study area only, up to 1000 m, but F. Hawkins also sighted one at 1300 m in the upper zone. Pairs and display flights observed, but no young birds. The species was sparsely distributed in the forest area, favoring emergent trees, natural gaps, and edges of clearings for foraging (Table 9-3). One was seen using its bill and feet to rummage in a large epiphytic fern.

Henst's Goshawk *Accipiter henstii*

The diet, natural density, and general ecology of this species are little known. Although it is widespread in Madagascar and cited to occur up to 1800 m (Langrand, 1990), it was not recorded above 1000 m in the study area, or in the nearby RNI de Marojejy (Safford & Duckworth, 1988), but F. Hawkins saw a female flying over the canopy at 1980 m. Below 1000 m, the records were sparse but distributed almost throughout the sample plot. There was no clear evidence that more than one pair was involved. All visual records of displaying birds were actually within 500 m from one another. Elsewhere, *Accipiter henstii* was seen inside the forest or only heard calling in or above the canopy. From what is known about the usual density of the similarly sized Holarctic *A. gentilis*, it would not be surprising that a single home range would cover 20 km² or more. Thus, the apparent rarity of *A. henstii* may be natural. Its upper elevation limit may be explained by the observed low abundance of large mammals and large birds above 1000 m. No hunting bird was seen in or along human-made clearings, where large birds (doves, pigeons, parrots, and rollers) were often more abundant than in the primary forest.

Madagascar Sparrowhawk *Accipiter madagascariensis*

This was the most widespread forest *Accipiter* in respect to habitat use, altitudinal range, and local density (Tables 9-2, 9-3). It was the only *Accipiter* recorded above 1100 m (up to at least 1450 m) and was seen hunting in the secondary growth of abandoned *tavys* and in the low, dense forest of upper ridges. This species favors dense canopy forest with a relatively open understory, where it perches at middle levels. Twice an adult was seen carrying a small, plucked bird (25 and 30 October), presumably to an occupied nest. The display flight was typically *Accipiter*-like, a silent male circling at moderate height over the forest with relatively slow, deep wingbeats.

Frances's Sparrowhawk *Accipiter francesii*

Considering the abundance of this small *Accipiter* and its widespread use of secondary woodlands elsewhere in Madagascar (Thiollay & Meyburg, 1981; Langrand, 1990), I expected to meet it more commonly and to find it in the secondary growth of abandoned *tavys* or plantations. It was relatively rare or unobtrusive and restricted to dense, tall natural forest edges and smaller gaps.

All records came from below 1100 m. A nest under construction was found on 20 October in a densely forested, humid ravine at 750 m. It was being built by the female 20 m off the ground in the main fork of a large tree. The male was observed bringing dry sticks on two occasions and also copulated with the female after the last delivery. From 25 October onward, the female appeared to be incubating. On 10 November, the female of another pair, at 950 m, was carrying prey, which suggests that she was already feeding fledglings (among accipiters, females usually do not hunt during the early nesting period). On 30 October, F. Hawkins found in the primary forest an adult male, with active testes, that had been killed by a predator (see Chapter 8, pp. 120–121).

Madagascar Buzzard *Buteo brachypterus*

The Madagascar Buzzard was the most conspicuous raptor in the reserve and also the most abundant and widespread along the elevational gradient. It also had the widest habitat niche use of all the resident raptor species (Table 9-3) and did not decrease in density between 700 and 1500 m. On the basis of visual surveys of the western area of the upper quadrat, two or more individuals were regularly hunting over the highest ridge of the mountain around 2000 m, where the forest cover was reduced to dense shrubs.

This species is primarily a forest-dweller, mostly hunting in the canopy, not in the low understory or systematically in tree-fall gaps or other natural openings, although it sometimes takes advantage of such sites. The large abandoned or cultivated clearings, dotted with isolated trees, were rarely used by *Buteo*, whereas elsewhere in Madagascar, such secondary or degraded woodlands seem to be used more readily, although much less than natural forests (Thiollay & Meyburg, 1981; Berkelman, 1994; René de Roland, 1994). Even the pair found breeding on the edge of a *tavy* (see below) was mostly hunting in the surrounding forest, sometimes along the forest edge and rarely inside the clearing, which was largely covered with a dense second growth. Among the possible reasons why the buzzards avoided the *tavys* (which may include suitability or accessibility of food), I suggest that the abundance of highly aggressive bird species (*Eurystomus*, *Dicrurus*, *Coracina*, and *Falco newtoni*), which never failed to harass any *Buteo* crossing their territory, may

have been a strong deterrent preventing buzzards from hunting successfully in the open.

The most commonly observed foraging behavior was a swift dive into the upper canopy by a bird gliding low above the forest in searching flight or darting into the foliage from an emergent tree where it was sitting. Several times, I saw a flock of Madagascar Blue Pigeons (*Alectroenas madagascariensis*) suddenly flushed by a *Buteo* pouncing in a tree crown, but it was not obvious that the pigeons themselves were actually the target. The only prey identified, in the feet of buzzards, were a probable small insectivore (*Microgale*), a small lemur (*Cheirogaleus*), and a snake. Other unindentified prey were small mammals and reptiles. Interestingly, the *Buteo* hunting over the low vegetation of the highest ridges between 1800 and 2000 m were mostly searching in flight, frequently hovering against the wind, a behavior I did not record at lower elevations.

At the time of the study, a majority of pairs were followed by flying, but still dependent, young. At least five pairs had single young, and two others had two fledglings. Four other pairs presumably still had unfledged young because they were seen carrying prey between 22 October and 11 November. An active nest was found on 8 November, at 15 m high in an isolated tree, dominating the secondary growth of a large *tavy* and 30 m away from the forest edge. The nest was placed on a large epiphytic fern (*Asplenium nidus*) and contained two full-grown nestlings that were fed and actively defended by both adults and were still in the nest on 13 November.

Madagascar Kestrel *Falco newtoni*

Every large clearing, either secondary growth, cultivated field, plantation, or large open area, around a settlement or along a road harbored a pair of this tame, small falcon. They were strictly associated with human-made openings and never entered the surrounding forest, even in small natural gaps. Some pairs had a hunting range that included two separate clearings and readily flew over the forest to join them. The density of this species (given in Table 9-2) refers to the area of the *tavys*.

The observed individuals mainly pounced on small ground prey, often from perches 5–15 m high on an isolated dead tree. They also showed an ability to chase small birds. The following captures were identified: 4 large insects (Orthoptera),

6 lizards, and 3 small passerines (once a male sunbird, *Nectarinia souimanga*).

Four nests were found and repeatedly checked between 20 October and 13 November. They were all in isolated tree holes from 6 to 14 m off the ground and were occupied by apparently brooding females. In every case, the female was regularly fed by the male. She left the hole when he brought the prey, fed on it in a nearby tree, and then went back into the cavity. Males often harassed *Buteo* and *Eurystomus*, and in turn they were mobbed by *Dicrurus forficatus* and *Leptopterus chabert*, which defended their respective nests.

Banded Kestrel   *Falco zoniventris*

This inconspicuous endemic falcon was recorded only between 900 and 1100 m in the lower part of the upper study area. The few sightings (Table 9-1) probably involved a single pair whose home range was centered on a forest patch between a road and an overgrown clearing. One individual was observed, at 10 m range, for 9 min, frantically dust-bathing on the road. New or old clearings, forest edges, and open forest were searched unsuccessfully for more individuals of this unaccountably rare species, which was described as fairly common around the RNI de Marojejy (Benson et al., 1976).

Eleonora's Falcon   *Falco eleonorae*

A single individual was hunting for flying insects over a large clearing near the road on 10 November, probably an early Palearctic wintering migrant. Up to four juveniles were seen at 1980 m by F. Hawkins between 28 November and 2 December.

Peregrine Falcon   *Falco peregrinus*

An adult male was observed on 12 November hunting low over the forest at 1200 m. There were several small cliffs on the western forested slopes of the upper study zone that may have offered convenient nest sites for this species.

Management and Conservation

Raptor species richness slowly decreased with elevation, as was found for the bird community as a whole (see Chapter 8). Only *Buteo* maintained a roughly similar abundance from the lowlands to near the summit. The other species for which enough data were obtained appeared most abundant in the lower part of the gradient and decreased with elevation. However, many of them within the RS d'Anjanaharibe-Sud did not reach the upper limit given by Langrand (1990) from elsewhere in Madagascar. This may be related to the high rainfall, humidity, and cloudiness found at upper elevations, which reduce the suitability of wet montane forests for lowland species. This also occurs in Asia and South America (Thiollay, unpubl. data).

Only part of the total area of the RS d'Anjanaharibe-Sud was actually surveyed. However, the study area covered the potentially richest part of this protected area. Most of the remaining unsurveyed forest within the reserve lay at an elevation similar to or higher than that of the study area (above 1000 m), and the few remaining patches, between 600 and 1000 m, were already cut over or highly degraded. There was no forest left below 650 m, so the true lowland forest community was not represented.

The lower part of our study area still contained all the forest raptor species known from the lowland rain forest of eastern Madagascar (Langrand, 1990), but it is likely that the abundance of some of them was lower than natural levels in undisturbed lowland primary forest, although comparative data are not yet available. This is suggested by the fact that several species were near the upper limit of their natural altitudinal range and that a substantial part of the natural forest was already cleared (*tavys*) or disturbed (mining). Consequently, the population size of the rarest species, which are also the species most dependent on primary forest tracts, may not be viable, especially if they are mostly restricted to the remaining montane forest, which is presumably a suboptimal habitat.

The lack of optimal habitat outside and even within the reserve was exemplified by the extreme case of *Eutriorchis*. The sighting of this critically endangered species (Collar et al., 1994) on the lower border of the reserve must be more likely considered as the last evidence of the presence of the species in the area if it cannot survive in the montane forest or in the too-degraded forest below 1000 m. Although the elevation of several localities where specimens had been obtained is not known, *Eutriorchis* still has not been recorded above 850 m (Safford & Duckworth, 1988) and 900 m (Dee, 1986). However, recent observations

on the Masoala Peninsula suggest that it is not fully intolerant of disturbed forest (Thorstrom et al., 1995). The recovery of now abandoned clearings at relatively low elevation may be a very long process. The policy of eliminating agricultural activities within the reserve's boundaries must be enforced and maintained over the long term if habitat-sensitive species are to be preserved. It is the only way to increase the area and continuity of lowland forest patches. Current monitoring of habitat selection, home range size, and reproductive success of *Eutriorchis* and other raptor species in the humid rain forest of Masoala Peninsula by the Peregrine Fund should provide critical data for better understanding the relationships between forest types, area, and management and the survival of the raptor community.

The decline in the number of resident species of raptors with elevation was not slowed by any addition of mid- or upper elevation specialists, as has happened with other birds. Species were lost along the altitudinal gradient more abruptly between 1000 and 1200 m. Nor was there any compensation in abundances, because no species was significantly more abundant at an intermediate or higher level than in the lowest part of the gradient. The two species surviving at the highest elevation were also the most abundant at the lowest levels.

Another cause for concern was the low rate of use of clearings by forest raptors in our study area. This was one of the lowest rates of use I have ever seen for this habitat type in any tropical country. With the exception of *Falco newtoni*, the local raptor species even foraged little along the edges of cultivated fields. As a result, any area of forest cleared for cultivation is almost completely lost for local resident raptors. Only *F. newtoni* benefits from such clearings and thus extends its range into the formerly forested areas. However, in other parts of Madagascar, all raptor species except *Eutriorchis*, considered here as a forest species, are seen more or less regularly in secondary forest, plantations, isolated forest patches, along forest edges, or in open woodlands (Goodman & Hawkins, pers. comm.). Why would they be less tolerant to deforestation in our study area? One possibility is that most clearings were recently abandoned and overgrown by dense secondary growth. Therefore, the ground level was often inaccessible, the midlevel vegetation was too dense for raptors, and the canopy level was restricted to widely scattered isolated trees. A special study in cultivated areas would be necessary to devise appropriate management options to maintain raptor diversity in such partly deforested areas. Our results suggest that the preservation of existing lowland forest patches has higher priority than preservation of larger tracts of montane forest.

Acknowledgments

Literature Cited

BENSON, C. W., J. COLEBROOK-ROBJENT, AND A. WILLIAMS. 1976. Contribution à l'ornithologie de Madagascar. Oiseau et Revue Française d'Ornithologie, **46:** 103–134.

BERKELMAN, J. 1994. The ecology of the Madagascar Buzzard, *Buteo brachypterus*, pp. 255–256. *In* Meyburg, B. U., and R. D. Chancellor, eds., Raptor Conservation Today. Pica Press, Near Robertsbridge, UK, xiv + 799 pp.

COLLAR, N. J., M. J. CROSBY, AND A. J. STATTERSFIELD. 1994. Birds to Watch 2. The World List of Threatened Birds. Birdlife International, Cambridge, UK. 407 pp.

DEE, T. J. 1986. The Endemic Birds of Madagascar. International Council for Bird Preservation, Cambridge, U.K. vi + 173 pp.

LANGRAND, O. 1990. Guide to the Birds of Madagascar. Yale University Press, New Haven, Conn., xi + 364 pp.

RENÉ DE ROLAND, L. A. 1994. Inventaire des rapaces utilisés comme indicateurs du milieu dans la partie occidentale de la presqu'île de Masoala. Mémoire DEA, Université d'Antananarivo, Madagascar.

SAFFORD, R., AND DUCKWORTH, W. 1988. A wildlife survey of Marojejy Nature Reserve, Madagascar. Study Report 40. International Council for Bird Preservation, Cambridge, UK. 172 pp.

THIOLLAY, J. M. 1989a. Area requirements for the conservation of rain forest raptors and game birds in French Guiana. Conservation Biology, **3:** 128–137.

———. 1989b. Censusing of diurnal raptors in a primary rain forest: Comparative methods and species detectability. Journal of Raptor Research, **23:** 72–84.

———. 1994. A world review of tropical forest raptors: Current trends, research objectives and conservation strategy, pp. 231–240. *In* Meyburg, B. U., and R. D.

Chancellor, eds., Raptor Conservation Today. Pica Press, Near Robertsbridge, UK.

THIOLLAY, J. M. AND B. U. MEYBURG. 1981. Remarques sur l'organisation d'un peuplement insulaire de rapaces: Madagascar. Alauda, **49:** 216–226.

THORSTROM, R., R. T. WATSON, B. DAMARY, F. TOTO, M. BABA, AND V. BABA. 1995. Repeated sightings and first capture of a live Madagascar Serpent-eagle *Eutriorchis astur.* Bulletin of the British Ornithologists' Club, **115:** 40–45.

Chapter 10

The Insectivores of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar

Steven M. Goodman[1] and Paulina D. Jenkins[2]

Abstract

Insectivores were surveyed on the eastern slopes of humid forest in the Réserve Spéciale d'Anjanaharibe-Sud at four elevational zones between 875 and 1950 m. Eleven species of tenrecs (*Setifer*, *Tenrec*, and nine species of *Microgale*) were documented within the reserve. An additional four species were also recorded on the western side of the reserve.

No species of insectivore occurred across the complete elevational transect. *Setifer setosus* and *Microgale principula* were restricted to the 875 m zone. The greatest species richness was found at 1260 and 1550 m with seven species of Tenrecidae (all *Microgale*). *Microgale dobsoni* was captured only at 1260 m. *Microgale soricoides*, *M. talazaci*, and *M. gymnorhyncha* were found in montane forest at 1260 and 1550 m, whereas *M. parvula* and *M. cowani* occurred in these two zones and approaching the summit at 1950 m. One species collected in montane forest of the reserve appears to be unrecognized and is described herein. Combining all sources of information, 16 species of Insectivora have been recorded within the reserve, 12 of which belong to the genus *Microgale*.

Résumé

Une enquête sur les insectivores de quatre zones situées sur un transect altitudinal entre 875 et 1950 m le long du versant oriental de la forêt humide sempervirente de la Réserve Spéciale d'Anjanaharibe-Sud a été réalisée. Onze espèces de tenrecs (*Setifer*, *Tenrec*, et neuf espèces de *Microgale*) ont été trouvées dans la réserve. Quatre espèces supplémentaires de *Microgale* ont été répertoriées sur le versant occidental de la réserve.

Aucune espèce d'insectivore n'a été trouvée sur l'ensemble des stations du transect altitudinal. *Setifer setosus* et *Microgale principula* présentaient une distribution restreinte à la station située à 875 m d'altitude. La plus grande diversité spécifique a été rencontrée à 1260 et 1550 m avec un total de sept espèces de Tenrecidae (toutes appartenant au genre *Microgale*). *Microgale dobsoni* était capturée seulement à 1260 m d'altitude, *Microgale soricoides*, *M. talazaci*, et *M. gymnorhyncha* ont été trouvées dans la forêt d'altitude à 1260 et 1550 m, alors que *M. parvula* et *M. cowani* étaient rencontrées dans ces deux zones et atteignaient presque les zones sommitales en étant présentes à 1950 m d'altitude. Une espèce collectée dans la forêt d'altitude de cette réserve semble être une nouvelle espèce et fait ici l'objet d'une description. En combinant toutes les sources d'information, 16 espèces d'insectivores ont été inventoriées au sein de la réserve, parmi lesquelles 12 appartiennent au genre *Microgale*.

[1] Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, IL 60605 U.S.A.
[2] The Natural History Museum, Cromwell Road, London SW7 5BD, United Kingdom.

Introduction

Before the current study, little was known about the small mammal community of the Réserve Spéciale (RS) d'Anjanaharibe-Sud. The only Insectivora listed by Nicoll and Langrand (1989) for the reserve are members of the endemic family Tenrecidae, *Tenrec ecaudatus* (Schreber, 1777) and *Setifer setosus* (Schreber, 1777). The Soricidae, the other family of Insectivora found in Madagascar, represented on the island by *Suncus madagascariensis* (Coquerel, 1848) and the introduced *Suncus murinus* (Linnaeus, 1766) has not been recorded from the reserve. In the nearby Réserve Naturelle Intégrale (RNI) de Marojejy, a high mountain zone just across the Andapa basin from the RS d'Anjanaharibe-Sud, *T. ecaudatus*, *Setifer setosus*, *Hemicentetes semispinosus* (Cuvier, 1798), *Microgale talazaci* (Major, 1896a), *M. pusilla* (Major, 1896b), and *M. cowani* (Thomas, 1882) have been recorded (Nicoll & Langrand, 1989). During the Mission Franco-Anglo-Américaine, a site "1 day W of Andapa" was visited (Rand, 1936), and material of *M. talazaci* was collected and is now deposited in the Muséum National d'Histoire Naturelle, The Natural History Museum, and the American Museum of Natural History. Other than these records, little is known about the insectivore community in the general Andapa area.

The current report is based on a small mammal survey recently undertaken by S. M. Goodman in the RS d'Anjanaharibe-Sud from October to November 1994. The purpose of the present study was to document the distribution of Tenrecidae along an elevational gradient on the slopes of the RS d'Anjanaharibe-Sud, specifically with regard to altitudinal distribution, density, and species richness of *Microgale* (Thomas, 1882).

The genus *Microgale* is the most speciose of the tenrec genera endemic to Madagascar. The genus was revised by MacPhee (1987), who established an effective taxonomy based chiefly on dental morphology. During recent small mammal surveys (Raxworthy & Nussbaum, 1994; Goodman et al., 1996), numerous samples of *Microgale* were collected, further increasing knowledge and allowing additional refinement of the taxonomy of the genus (Jenkins et al., 1996, 1997).

The RS d'Anjanaharibe-Sud survey commenced in lowland forest at 875 m, progressing to montane forest at 1260 and 1550 m and to upper montane forest at 1950 m. Only one species of *Microgale*, *M. principula* (Thomas, 1926), was collected at the lower altitude, while eight other species were found in the montane and upper montane zones. Information on these nine species, including one believed to be undescribed, as well as other species of Tenrecidae found within the reserve, is given below.

Materials and Methods

Two principal techniques were used to trap insectivores in the four surveyed transect zones (at 875, 1260, 1550, and 1950 m above sea level): pitfall traps and standard small mammal live traps. The pitfall traps were composed of 11 plastic buckets (275 mm deep, 290 mm top internal diameter, and 220 mm bottom internal diameter), sunk in the ground at 10 m intervals with the upper rims flush with ground surface level. Small holes (2 mm diameter) were drilled in the bottom of the buckets to allow water drainage. A black plastic drift fence, 100 m long and 0.5 m high, was erected in a vertical position and stapled to thin wooden stakes. The fence bottom was buried 50 mm into the ground using leaf litter or soil and positioned to run across the middle of each pitfall trap. Pitfall buckets were positioned at 10 m intervals. Within each elevational zone, three lines were installed (valley bottom, slope, and ridge crest). Each line was checked in the morning soon after dawn and again in the late afternoon. After rain the buckets were sponge-dried. A bucket in place for a 24-hr period is referred to as a "bucket-day" (dawn to dawn). This is the same technique we have systematically used over the past few years in Madagascar (Raxworthy et al., 1994; Jenkins et al., 1996; Raxworthy & Nussbaum, 1996). The period of the survey coincided with the season when all tenrecs are presumed to be active (Stephenson, 1994).

In each elevational zone surveyed, trap lines were in operation for a minimum of five nights. Each trap line consisted of Sherman live traps (9 × 3.5 × 3 inches) and National live traps (16 × 5 × 5 inches) in a ratio of 4:1. Traps were baited daily, generally between 15:00 and 17:00 hr, with a fresh mixture of finely ground peanut butter and corn grain mixed in proportions to make a paste. Traps were visited at least twice per day, once at dawn and in the late afternoon. A "trap-night" is defined as one trap in use for a 24-hour period (dawn to dawn).

Captured animals were either released or pre-

pared as standard museum skins with associated skulls and skeletons, fluid-preserved carcasses, or full skeletons. Voucher specimens are deposited in the Field Museum of Natural History, Chicago, and the Département de Biologie Animale, Université d'Antananarivo, Antananarivo.

Measurements

Cranial measurements were taken using dial calipers and a microscope measuring stage. The dental nomenclature follows that of Mills (1966), Swindler (1976), Butler and Greenwood (1979), and MacPhee (1987). Dental notations are given in parentheses in the text; premaxillary and maxillary teeth are denoted by uppercase letters, and mandibular teeth are denoted by lowercase letters. The following measurements were made of specimens in the flesh or from prepared crania. Abbreviations and definitions for these measurements (all in millimeters with the exception of weight, which is in grams) are as follows:

BB = breadth of braincase, the greatest distance measured across the squamosals
CIL = condyloincisive length, cranial length from first upper incisor to occipital condyle
EL = ear length, measured from the notch at the base of the ear to the distalmost edge of the pinna
HB = head and body length, measured from the tip of the nose to the distalmost point of the body (at base of tail)
HF = hindfoot length, measured from the back edge of the heel to the tip of the longest toe (not including claw)
I1–P3 = length of anterior upper teeth, from anterior of first upper incisor to anterior of second upper premolar
TL = tail length, measured from the base of the tail (at right angles to the body) to the end of the distalmost vertebra; does not include terminal hair tufts
TOTL = total length of body and tail, measured from the tip of the nose to the end of the distalmost tail vertebra; animal is positioned on its back straight with vertebrae parallel to ruler but not stretched out
UTL = upper toothrow length, from anterior of first upper incisor to posterior of third

upper molar, parallel to the long axis of the skull
WT = weight, measured in grams with Pesola spring scales; animals weighing less than 10 g were weighed to within 0.2 g, and those weighing between 10 and 100 g were weighed to within 0.5 g

Reproductive condition was recorded for males as length × width of the testes and degree of convolution of the epididymis. Females were noted as nonperforate or perforate and as nonparous or parous, and the number and location of any embryos and placental scars were recorded. The mammary formula is presented as the number of paired axial, abdominal, or inguinal teats.

The following age classes are recognized: "Infant" includes individuals in which the deciduous antemolar dentition and the molars are not fully erupted; the premaxillary, parietal, and basioccipital sutures are unfused. "Juvenile" includes individuals in which the molars are fully erupted and the deciduous antemolar dentition is erupted and in the process of replacement by the permanent teeth; cranial sutures are in the process of fusing. The eruption sequence of the permanent teeth has been subdivided into four stages by MacPhee (1987); these stages have been accepted in this chapter unless otherwise stated. "Adult" includes individuals with fully erupted permanent dentition; cranial sutures are generally fused, although their position is more or less clearly marked.

Other abbreviations used are as follows:

PN   = Parc National
RNI = Réserve Naturelle Intégrale
RS   = Réserve Spéciale
BM(NH) = Natural History Museum, London (formerly British Museum (Natural History)
FMNH = Field Museum of Natural History, Chicago
MCZ = Museum of Comparative Zoology, Harvard
MNHN = Muséum National d'Histoire Naturelle, Paris
UMMZ = University of Michigan, Museum of Zoology, Ann Arbor
C/c = canine
d   = deciduous
I/i = incisor
M/m = molar
P/p = premolar

Systematic Section

Subfamily Tenrecinae
Setifer setosus (Schreber, 1777)

HOLOTYPE—Unknown.

TYPE LOCALITY—Madagascar.

REFERRED MATERIAL—FMNH 154033, 154034, 154230, 154231, 154232, 154233, 154234, 154235: 6.5 km SSW of Befingitra, 14°45'S, 49°30'E, 875 m.

KEY FEATURES (see Appendix 10-1, p. 161)—Dorsum covered with spines. Skull moderately robust, dorsal profile curved in lateral view; rostrum deep and broad; interorbital region broad and elongated; braincase short, supraoccipital crest present. Two lower incisors present; dental formula 2/2 1/1 3/3 3/3 = 36; first upper incisors well developed, slightly shorter than upper canines; short diastemata on either side of upper canines and first lower premolar.

POPULATION STRUCTURE AND REPRODUCTION—The sex ratio of females to males was 1:4. Mammary formula: 1-2-2 (n = 2).

REMARKS—At 875 m four *Setifer* were obtained in pitfall traps; five individuals were obtained in live traps. All of the latter group were captured on the ground, generally in areas with thick ground leaf litter. Nicoll and Langrand (1989) previously reported this species from the reserve. It has a broad range across the island from Antsiranana to the Tolagnaro and Toliara regions.

Tenrec ecaudatus Schreber, 1777

HOLOTYPE—Unknown.

TYPE LOCALITY—Madagascar.

KEY FEATURES (see Appendix 10-1, p. 161)—The largest of the Tenrecinae. Dorsal pelage of coarse, bristly hair intermixed with spines. Skull elongated; rostrum with deep sockets in ventrolateral region of the premaxillae, which accommodate the lower canines when the jaw is closed; interorbital region narrow, elongated; braincase short, narrow, angular, pronounced sagittal and supraoccipital crests form deep posterodorsal flanges. Three lower incisors present; dental formula 2/3 1/1 3/3 3/3 = 38; upper and lower canines very long, robust, and prominent; pronounced diastemata on either side of upper canines and posterior to lower canines; short diastemata posterior to first upper and lower premolars.

REMARKS—This widespread species was ob-

served on two occasions at 875 m and thrice at 1260 m. No specimen was collected. Nicoll and Langrand (1989) also reported this species from the reserve.

Microgale cowani Thomas, 1882

HOLOTYPE—BM(NH) 82.3.1.25, adult female body in alcohol, skull extracted, collected mid-March to mid-February 1880 by the Reverend W. Deans Cowan.

TYPE LOCALITY—Ankafana Forest, eastern Betsileo (Ankafana = Ankafina, Fianarantsoa, and Fianarantsoa Province, 21°12'S, 47°12'E; see MacPhee, 1987; Carleton & Schmidt, 1990).

REFERRED MATERIAL—FMNH 154020, 154021, 154022, 154195: 9.2 km WSW of Befingitra 14°44'S, 49°27'E, 1260 m; FMNH 154023, 154024, 154025, 154026, 154196, 154197, 154198, 154199, 154200, 154201, 154204: 11 km WSW of Befingitra, 14°44'S 49°26'E, 1550 m; FMNH 154202, 154203, 154205, 154206, 154207: 12.2 km WSW of Befingitra, 14°44'S, 49°26'E, 1950 m.

KEY FEATURES (see Table 10-1 and Appendix 10-2, p. 161)—Medium-sized *Microgale*, tail moderately short, shorter or subequal to HB. Pelage dark brown dorsally, gray ventrally with a reddish brown wash; tail bicolored, dark brown dorsally, sharply demarcated from paler reddish buff venter. Skull medium in size, rostrum elongated; pronounced diastemata separate teeth of upper anterior dentition from first upper incisor (I1) to second upper premolar (P3), also on either side of lower canine (c) and first lower molar (p2). All elements of talonid of third lower molar (m3) present, including hypoconid, entoconid ridge, talonid basin, and entoconid.

MEASUREMENTS—External and cranial measurements are presented in Table 10-1.

VARIATION—No interpopulation variation in size or pelage color was observed.

POPULATION STRUCTURE AND REPRODUCTION—The sex ratio of females to males was 1:1.5. The ratio of adults to juveniles was 1:1.5. Juveniles were not significantly smaller than adults in body or cranial size, although they were clearly lighter in body weight (see Table 10-1). All but one of the juveniles were dentally immature, with all molars fully erupted and either with a fully deciduous anterior dentition or only the third incisors in the process of replacement (stage 1 of MacPhee, 1987:13); the exception was a specimen at stage

Table 10-1. Dimensions of *Microgale* from RS d'Anjanaharibe-Sud.*

Taxon	HB	TL	HF	EL	WT	CIL	UTL	BB
Microgale cowani								
Adults	77–87 82.4 ± 3.00 (8)	60–75 66.3 ± 4.43 (7)	15–17 16.0 ± 0.71 (8)	13–16 14.5 ± 1.00 (8)	11.5–16.0 12.8 ± 1.41 (8)	22.3, 22.8 (2)	10.6, 10.8 (2)	10.1, 10.3 (2)
Juveniles	73–87 79.4 ± 4.65 (12)	61–76 67.3 ± 4.76 (12)	15–17 16.3 ± 0.62 (11)	14–16 14.4 ± 0.64 (12)	9.5–11.5 10.5 ± 0.72 (12)	22.0–22.9 22.4 ± 0.31 (5)	10.2–10.6 10.5 ± 0.14 (5)	9.7–10.4 10.0 ± 0.27 (5)
Microgale longicaudata								
Adults	72, 74 (2)	148, 151 (2)	17 (2)	15 (2)	8.0, 9.5 (2)	21.3, 21.5 (2)	10.2, 10.4 (2)	8.7, 9.1 (2)
?long./maj.† Juveniles	65 (1)	149 (1)	18 (1)	18 (1)	5.5 (1)	19.2 (1)	9.1 (1)	8.0 (1)
Microgale principula								
Juveniles	79, 80 (2)	151, 171 (2)	19 (2)	15, 16 (2)	8.5, 10.5 (2)	22.7, 23.2 (2)	10.1, 10.8 (2)	9.3, 9.4 (2)
Microgale parvula								
Adults	58–61 60.3 ± 1.30 (4)	51–60 55.5 ± 3.35 (4)	10 ± 0 (4)	8–9 8.75 ± 0.43 (4)	3.1–3.9 3.4 ± 0.33 (4)	16.0–16.8 16.3 ± 0.32 (4)	7.3–7.6 7.4 ± 0.11 (4)	6.5–6.7 6.6 ± 0.08 (4)
Juveniles	58 (1)	54 (1)	10 (1)	8 (1)	2.4 (1)	15.7 (1)	7.1 (1)	6.7 (1)
Microgale dobsoni								
Adults	100–111 104 ± 3.96 (7)	102–128 114.7 ± 7.8 (7)	21–24 22.3 ± 1.03 (7)	16–19 17.9 ± 0.99 (7)	20.5–30 25.5 ± 2.77 (7)	28.8–31.3 30.1 ± 0.72 (7)	14.2–15.6 15.2 ± 0.43 (7)	10.9–11.4 11.3 ± 0.16 (7)
Juveniles	101–112 106.7 ± 4.50 (3)	112–120 115.3 ± 3.40 (3)	22–23 22.7 ± 0.47 (3)	18–19 18.3 ± 0.47 (3)	23.5–31.5 26.7 ± 3.47 (3)			
Microgale talazaci								
Adults	107–124 113.3 ± 6.57 (4)	126–144 136.6 ± 6.25 (5)	23–26 24.6 ± 1.02 (5)	19–20 19.4 ± 0.49 (5)	31.5–39.5 36.0 ± 2.87 (4)	34.8–36.0 35.4 ± 0.43 (4)	17.3–18.1 17.8 ± 0.29 (4)	12.2–12.7 12.4 ± 0.18 (4)
Microgale soricoides								
Adults	85–103 90.4 ± 6.80 (5)	84–97 92.6 ± 4.63 (5)	17–18 17.4 ± 0.49 (5)	15–17 16 ± 0.63 (5)	16–22 19.2 ± 2.06 (5)	25.5–26.3 25.9 ± 0.29 (4)	12.4–12.8 12.6 ± 0.15 (4)	10.6–11.1 11.0 ± 0.22 (4)
Juveniles	84 (1)	94 (1)	17 (1)	15 (1)	14 (1)	25.6 (1)	12.1 (1)	11.0 (1)

(*cont.*)

TABLE 10-1. *Continued.*

Taxon	HB	TL	HF	EL	WT	CIL	UTL	BB
Microgale gymnorhyncha								
Adults	100, 101 (2)	63, 71 (2)	16, 18 (2)	14, 15 (2)	17.5, 20 (2)	27.1, 27.7 (2)	13.8, 14.5 (2)	11.0, 11.3 (2)
Juveniles	84–94 88.8 ± 3.96 (4)	62–70 65.3 ± 2.95 (4)	17–18 17.5 ± 0.5 (4)	13–14 13.5 ± 0.5 (4)	11.5–16.5 14 ± 2.5 (4)	24.6–27.4 26.2 ± 1.15 (4)	13.2–14.5 13.8 ± 0.52 (4)	10.3–10.5 10.4 ± 0.07 (4)
Microgale monticola								
Adults	81–92 85.8 ± 4.35 (5)	105–113 109.5 ± 2.43 (6)	20–21 20.8 ± 0.37 (6)	15–16 15.7 ± 0.47 (6)	13.5–17.5 15.5 ± 1.38 (5)	25.5–25.8 25.7 ± 0.12 (5)	12.4–12.8 12.6 ± 0.15 (5)	10.5–11.1 10.9 ± 0.21 (5)
Infant	62 (1)	80 (1)	19 (1)	12 (1)	7.5 (1)	20.6 (1)		9.8 (1)

* Measurements are given as the range, followed by the mean ± SD and the sample size (in parentheses). See "Materials and Methods" for definitions of abbreviations. For samples of two or less only the measurements are presented.
† *Microgale longicaudata/majori.* See text (p. 144) for a discussion of this animal.

2, with the first and third incisors and the first and third premolars erupting. One adult female was lactating. Another female (FMNH 154021), despite having a fully deciduous anterior dentition and unfused premaxillary and basioccipital sutures, was reproductively adult because the mammae were slightly enlarged, two placental scars were present in the left oviduct, and one scar was present in the right oviduct. Mammary formula: 1-0-2 (n = 6).

REMARKS—See Jenkins et al. (1996) for redefinition of this species and an augmented description. Given the taxonomic complications of the name "*cowani*" in the literature and the various treatments of its species limits (see MacPhee, 1987; Stephenson, 1995), it is difficult to assess the northern limit of *cowani*. However, on the basis of material we have examined and the redefinition of this species by Jenkins et al. (1996), the specimens from the RS d'Anjanaharibe-Sud mark the northern known limit of its range.

Microgale longicaudata Thomas, 1882
Microgale majori Thomas, 1918; MacPhee, 1987

HOLOTYPE—BM(NH) 82.3.1.15, adult female, body in alcohol, skull extracted, collected mid-March to mid-February 1880 by the Reverend W. Deans Cowan.

TYPE LOCALITY—Ankafana Forest, eastern Betsileo (Ankafana = Ankafina, Fianarantsoa, and Fianarantsoa Province, 21°12′S, 47°12′E; see MacPhee, 1987; Carleton & Schmidt, 1990).

REFERRED MATERIAL—FMNH 154005: 9.2 km WSW of Befingitra, 14°44′S, 49°27′E, 1260 m; FMNH 154006: 11 km WSW of Befingitra, 14°44′S, 49°26′E, 1550 m; FMNH 154220: 12.2 km WSW of Befingitra, 14°44′S, 49°26′E, 1950 m.

KEY FEATURES (see Table 10-1 and Appendix 10-2, p. 161)—Small in size, tail very long, more than twice as long as HB; distal portion of tail naked and transversely wrinkled on dorsal surface; fifth hind digit elongated, subequal in length to second digit. Dorsal pelage reddish brown, venter gray with bright reddish buff or buff wash. Skull small, rostrum moderately short; braincase moderately narrow and long. Diastemata present between I1 and second upper molar (I2) and either side of upper canine (C) and first upper premolar (P2); well-developed anterior and posterior accessory cusps present on I2, C, and P2; C subequal to or taller than I1; third upper premolar (P4)

scarcely greater in crown height than P3. Lower p2 caniniform. Talonid of m3 with low hypoconid, hypoconulid well developed, narrow talonid basin, reduced entoconid ridge, and entoconid absent.

MEASUREMENTS—External and cranial measurements are presented in Table 10-1.

VARIATION—Marked variation in size between populations was observed. Specimens from RS d'Anjanaharibe-Sud are larger than those from RNI d'Andringitra (see Jenkins et al., 1996) and PN de Mantady.

POPULATION STRUCTURE AND REPRODUCTION—The single juvenile had fully erupted molars but completely deciduous anterior dentition and unfused premaxillary and basioccipital sutures. Two adult females were collected during the survey; both were perforate, and one was lactating. Mammary formula: 1-0-2 (n = 1).

REMARKS—*Microgale longicaudata* is a widespread shrew tenrec known from scattered localities from PN de la Montagne d'Ambre in the north to the RNI d'Andringitra in the south (Jenkins et al., 1996). Although this sample is too small for valid conclusions, the size difference between the small juvenile (FMNH 154005) and the large adults (FMNH 154006 and 154220) appears greater than that likely to be attributable to growth. In addition, the adult specimens from RS d'Anjanaharibe-Sud, in common with those from Ankafina and Amboanara considered to represent *M. longicaudata* by Thomas (1918), are larger than those from RNI d'Andringitra, PN de Mantady, and the other specimens from Ankafina considered by Thomas to represent *M. majori*. Although MacPhee (1987) synonymized *M. majori* with *M. longicaudata*, this evidence tends to support the original view of Thomas (1918) that *M. majori* may be a separate species distinguishable by its smaller size from *M. longicaudata*.

The only individual of this species captured at 1550 m was obtained in a Sherman live trap placed on a moss-covered vine 1.5 m above the ground. In the literature on *Microgale longicaudata*, there has been speculation, based on external morphology (Thomas, 1918; Eisenberg & Gould, 1970; MacPhee, 1987) and skeletal structure (Dobson, 1882), that its long and modified tail might have some prehensile capabilities. We are now able to confirm this ability: a captive animal was able to dangle by the tip of its tail from a thin branch for at least 10 sec (see Fig. 10-1) using only the very distal tip of its tail to grip the branch.

Microgale longicaudata and *M. principula* share many presumed derived morphological adaptations, particularly the long prehensile tail, and have similar cranial and dental morphologies. Although no phylogenetic analysis of the genus has been conducted to date, we strongly suspect that these two taxa are closely related and fill similar ecological niches. On the slopes of the RS d'Anjanaharibe-Sud, these two species replace one another, with *principula* occurring in lowland forest and *longicaudata* on the higher slopes. We have no evidence that they occur in microsympatry on the mountain. To our knowledge, this is the second reported case of these two species occurring in close proximity; both species have also been recorded from PN de Mantady (see Jenkins, 1993).

Microgale principula Thomas, 1926

Microgale sorella Thomas, 1926; MacPhee, 1987

HOLOTYPE—BM(NH) 25.8.3.15, adult female, body in alcohol, skull extracted, collected by C. Lamberton.

TYPE LOCALITY—Midongy du Sud, SE Madagascar (Midongy Atsimo, 23°35'S, 47°01'E; see MacPhee, 1987).

REFERRED MATERIAL—FMNH 154003, 154004: 6.5 km SSW of Befingitra, 14°45'S, 49°30'E, 875 m.

KEY FEATURES (see Table 10-1 and Appendix 10-2, p. 161)—Medium-sized *Microgale*, tail very long, more than twice as long as HB; distal portion of tail naked and transversely wrinkled on dorsal surface; fifth hind digit elongated, subequal in length to second digit. Pelage distinctly bicolored, reddish brown dorsally, gray with buff wash ventrally. Skull medium in size, rostrum moderately short and broad, braincase moderately narrow. Short diastemata between I1 and I2, and on either side of C and P2, I2 and third upper incisor (I3) more or less in contact; well-developed anterior and posterior accessory cusps present on I2, C, and P2; I1 greater in crown height than C; P4 distinctly greater in crown height than P3. Lower p2 moderately caniniform. Talonid of m3 with low hypoconid, well-developed hypoconulid, broad talonid basin, reduced entoconid ridge, entoconid absent.

MEASUREMENTS—External and cranial measurements are presented in Table 10-1.

VARIATION—The sample is too small for meaningful comments on variation.

POPULATION STRUCTURE AND REPRODUCTION—

FIG. 1. Photograph of *Microgale longicaudata* (FMNH 154005) captured in the 1260 m zone and hanging suspended by its distally prehensile tail. The photograph was staged in the sense that the animal's tail was manipulated as the single point of contact with the branch. Once the animal was released in this position, it was able to remain suspended for more than 10 sec. (Photograph by Brian Fisher.)

The sample contained two juveniles, one at stage 2 and the other at stage 3 of dental development (MacPhee, 1987); the sex ratio was 1:1. The testes of FMNH 154004, in which P3 and p3 were erupting, measured 7 × 5 mm with a convoluted epididymides, so the specimen was probably reproductively active while still retaining some deciduous teeth.

REMARKS—This species was previously known to occur from the RS d'Ambatovaky (16°51′S, 49°08′E) in the north-central portion of the eastern humid forest (Jenkins, 1992) to the Grotte d'Andrahomana in the extreme south (MacPhee, 1987). The specimens from the RS d'Anjanaharibe-Sud mark the most northerly locality to date from which this species has been recorded.

Microgale parvula G. Grandidier, 1934
Microgale pulla Jenkins, 1988

HOLOTYPE—MCZ 45465, juvenile male, body in alcohol, skull extracted, collected by M. Drouhard.

TYPE LOCALITY—Environs of Diego-Suarez (Antsiranana, ca. 12°16′S, 49°18′E, see MacPhee, 1987; probably Montagne d'Ambre, see Jenkins et al., 1997).

REFERRED MATERIAL—FMNH 154007, 154217: 9.2 km WSW of Befingitra, 14°44′S, 49°27′E, 1260 m; FMNH 154008: 11 km WSW of Befingitra, 14°44′S, 49°26′E, 1550 m; FMNH 154218, 154219: 12.2 km WSW of Befingitra, 14°44′S, 49°26′E, 1950 m.

KEY FEATURES (see Table 10-1 and Appendix 10-2, p. 161)—Very small, TL slightly shorter than HB. Dorsal pelage dark brown, ventral pelage dark gray-brown, tail uniform dark gray. Skull very small and delicate, rostrum slender, braincase shallow and long, occipital condyles posterodorsally orientated. Diastemata between I1 and I2 and either side of C and P2; anterior and posterior accessory cusps present on I2, I3, and P2. Diastema between c and p2. Talonid of m3 with well-developed hypoconulid but reduced hypoconid, entoconid and entoconid ridge, and narrow, shallow talonid basin.

MEASUREMENTS—External and cranial measurements are presented in Table 10-1.

VARIATION—There is no obvious interpopulation variation in size or pelage coloration.

POPULATION STRUCTURE AND REPRODUCTION—The sample contained four adults and one juvenile, and the sex ratio of females to males was 1:1.5. The juvenile, which had a fully deciduous anterior dentition, was within the size range of the adults in most dimensions, except body weight, CIL, and UTL, in which it was smaller (see Table 10-1). One of the two adult females was lactating, both were perforate, and the mammary formula was 1-0-2 (n = 1). The testes of one adult male measured 3 × 2 mm with convoluted epididymides.

REMARKS—See Jenkins et al. (1996; 1997) for redefinition and augmented description of this species as well as for information on its range. This species is now known from the far north in the PN de la Montagne d'Ambre (Raxworthy & Nussbaum, 1994) to the extreme southern limit of the eastern humid forest in the Vohimena Mountains (UMMZ) and Anosyenne Mountains (FMNH).

Microgale dobsoni Thomas, 1884
Nesogale dobsoni Thomas, 1918

HOLOTYPE—BM(NH) 84.10.20.1, immature male, in alcohol, skull extracted. Collected February or March 1884 by W. Waters.

TYPE LOCALITY—Nandésen forest, Central Betsileo (Nandihizana, 10 miles S of Ambusitra, manuscript note in Thomas' private copy of original description, archived in BM(NH); Nandihizana, ca. 20 miles (30 km) SSW of Ambositra, see MacPhee, 1987; estimated as ca. 20°50'S, 47°10'E).

REFERRED MATERIAL—FMNH 154015, 154016, 154208, 154209, 154210, 154211, 154212, 154213, 154214, 154215: 9.2 km WSW of Befingitra, 14°44'S, 49°27'E, 1260 m.

KEY FEATURES (see Table 10-1 and Appendix 10-2, p. 161)—Large, TL subequal to or longer than HB. Dorsal pelage brown, venter gray with buff wash. Skull large and robust, sutures fused and obscure; rostrum moderately broad, interorbital region long; braincase angular, superior articular facets very prominent, supraoccipital crests well developed; occipital region reduced. Diastemata between I1 and I2 and between I3 and C. Upper I1 larger than I2, i2 considerably larger than canine. Talonid of m3 reduced, hypoconid low, hypoconulid prominent, entoconid ridge and talonid basin poorly defined, entoconid absent.

MEASUREMENTS—External and cranial measurements are presented in Table 10-1.

VARIATION—No obvious variation in size is evident.

POPULATION STRUCTURE AND REPRODUCTION—The ratio of juveniles to adults in the sample was 1:2.3, and the sex ratio was 1:1. There was no indication of sexual dimorphism in size in this small sample, except in body weight, where the females were notably heavier (20.5–25.5, mean 23.8 ± 2.05, n = 4 for males; 26.0–30.0, mean 27.8 ± 1.65, n = 3 for females), although the sample is too small to be statistically significant. The size range of adults and juveniles was similar, although the range and mean in body weight of the juveniles actually exceeded that of the adults (see Table 10-1); it is suggested that this may be an anomalous result due to the small sample size. One of the adult females was lactating and had two placental scars in the left oviduct and three scars in the right oviduct. Mammary formula: 1-1-2 (n = 5).

REMARKS—Two of the *Microgale dobsoni* obtained in the 1260 m zone were captured in Sherman traps. Both were taken on consecutive nights in the same trap placed on the ground next to a small tree with a hole in the base. One *M. talazaci* was taken in the same trap set, which shows that these two species, at least on occasion, have overlapping home ranges.

This species is widespread and is now known from Manohilahy, 17°16'S, 48°01'E (Eisenberg & Gould, 1970), to Antampona (MacPhee, 1987). The specimens from the RS d'Anjanaharibe-Sud mark the northernmost record to date. This species and *M. talazaci*, the largest shrew-tenrecs, are known to be sympatric at several sites, including RS d'Analamazaotra (Eisenberg & Gould, 1970), RS d'Ivohibe (MacPhee, 1987), and on the Ankaratra Massif (BM(NH), FMNH, and MNHN).

Microgale talazaci Major, 1896a
Nesogale talazaci Thomas, 1918

HOLOTYPE—BM(NH) 97.9.1.107, adult female, skin, skull, and skeleton. Collected 22 May 1896 by C. I. Forsyth Major.

TYPE LOCALITY—Forest of the Independant Tanala of Ikongo, in the neighborhood of Vinanitelo, 1 day's journey S of Fianarantsoa, 21°44'S, 47°16'E.

REFERRED MATERIAL—FMNH 154017, 154224, 154225, 154226: 9.2 km WSW of Befingitra, 14°44′S, 49°27′E, 1260 m; FMNH 154018: 11 km WSW of Befingitra, 14°44′S, 49°26′E, 1550 m.

KEY FEATURES (see Table 10-1 and Appendix 10-2, p. 161)—Very large, TL longer than HB. Dorsal pelage brown, venter gray with reddish buff wash. Skull very large and robust, sutures fused and obscure; rostrum broad, interorbital region long, parallel sided; braincase angular, short relative to cranial length, superior articular facets very prominent, supraoccipital crests well developed, occipital region very reduced, occipital condyles visible in dorsal view. Small diastemata between I1 and I2 and between I3 and C. Upper I1 larger than I2, i2 considerably larger than canine. Talonid of m3 reduced, hypoconid low, hypoconulid well marked, entoconid ridge and talonid basin poorly defined, entoconid absent.

MEASUREMENTS—External and cranial measurements are presented in Table 10-1.

VARIATION—There is no obvious variation in size.

POPULATION STRUCTURE AND REPRODUCTION—The sample consisted of five adults, with a sex ratio of 1:3 (females to males). The testes of two males measured 5 × 3 mm and 10 × 6 mm, both with convoluted epididymides. The female was perforate, with a mammary formula of 1-1-2.

REMARKS—At 1260 m one *Microgale talazaci* was trapped in a Sherman trap placed on the ground at the base of a small tree with a hole in its base. The only individuals of this species captured within the 1550 m elevational zone were taken on the ground in Sherman live traps; one individual was collected in a trap placed at the opening of a small hole under a large boulder, and a second individual was collected at the base of a small tree with a cavity under the roots. *Microgale talazaci* is known from humid forests at a range of elevations from the Antsiranana region south to Vondrozo (MacPhee, 1987) and west to the Sambirano (BM(NH)).

Microgale soricoides Jenkins, 1993

HOLOTYPE—BM(NH) 91.565, adult male in alcohol, skull extracted. Collected 13 April 1991 by C. J. Raxworthy.

TYPE LOCALITY—Mantady National Park (PN de Mantady), ca. 15 km north of Périnet (Andasibe), 18°51′S, 48°27′E, in primary rain forest, 1100–1150 m.

REFERRED MATERIAL—FMNH 154027, 154029, 154221, 154222, 154223: 9.2 km WSW of Befingitra, 14°44′S, 49°27′E, 1260 m; FMNH 154030: 11 km WSW of Befingitra, 14°44′S, 49°26′E, 1550 m.

KEY FEATURES (see Table 10-1 and Appendix 10-2, p. 161)—Size large, TL subequal to or longer than HB. Pelage light buff brown dorsally, gray-brown ventrally with reddish buff wash. Skull moderately large and robust, rostrum and interorbital region broad, braincase short and broad; supraoccipital ridge present. First I1 markedly robust and pro-odont. First i1 and i2 robust and procumbent, i2 smaller than i1 but larger than c. First upper and lower premolars very small with a single root. Talonid of m3 reduced to very low hypoconid, oblique crest, and prominent hypoconulid.

MEASUREMENTS—External and cranial measurements are presented in Table 10-1.

VARIATION—There is no evidence of size variation in the small sample available.

POPULATION STRUCTURE AND REPRODUCTION—The age structure in the sample consisted of one juvenile with a fully deciduous anterior dentition and five adults, and the sex ratio (males to females) was 1:2. In size, the juvenile was at the lower part of the adult range and weighed less than any of the adults (see Table 10-1). One adult male had testes measuring 5 × 5 mm with convoluted epididymides. Mammary formula: 1-0-2 (n = 1); 1-1-2 (n = 2).

REMARKS—This species is now known from three localities, the type locality in the PN de Mantady (18°51′S, 48°27′E), the RNI d'Andringitra (Jenkins et al., 1996), and the RS d'Anjanaharibe-Sud, which marks the northernmost record to date.

Microgale gymnorhyncha Jenkins, Goodman and Raxworthy 1996

Microgale gracilis (Major): MacPhee, 1987, in part

HOLOTYPE—FMNH 151807, adult female in alcohol, skull extracted (field number SMG 6697), collected 13 December 1993 by S. M. Goodman and C. J. Raxworthy.

TYPE LOCALITY—38 km S of Ambalavao, RNI d'Andringitra, on ridge E of Volotsangana River, Fianarantsoa Province, 22°11′39″S, 46°58′16″E, 1625 m.

REFERRED MATERIAL—FMNH 154028, 154216: 9.2 km WSW of Befingitra, 14°44′S, 49°27′E,

1260 m; FMNH 154009, 154010, 154011, 154031: 11 km WSW of Befingitra, 14°44'S, 49°26'E, 1550 m.

KEY FEATURES (see Tables 10-1 and Appendix 10-2, p. 161)—Large, TL shorter than HB. Dorsal pelage dark brown, dark gray-brown ventrally. Muzzle very long, forming a proboscis; rhinarium very large with transversely striated naked region. Eyes very small. Ears small, virtually concealed in pelage. Forefeet broad, claws enlarged. Skull long, moderately gracile; rostrum slender and elongated; braincase short and broad. Dentition moderately reduced with long diastemata between all anterior teeth from I1 to P3 and i2 to p3; talonid of m3 slightly reduced; talonid basin, hypoconid, hypoconulid, and entoconid ridge present, entoconid indicated.

MEASUREMENTS—External and cranial measurements are presented in Table 10-1.

VARIATION—The pelage of juveniles is duller and grayer than that of adults, which are more speckled brown on the head and the anterior part of the dorsum. There is some evidence from the small samples available that specimens from RS d'Anjanaharibe-Sud average larger than those from RNI d'Andringitra (see Table 10-1 and Jenkins et al., 1996).

POPULATION STRUCTURE AND REPRODUCTION—The adult to juvenile ratio in the sample was 1:2, and the ratio of females to males was 1:1.5. The juveniles were all dentally immature, with the third molars still in the process of eruption in two specimens, whereas the other two had fully deciduous anterior dentitions but erupted molars. In size, the juveniles fell below or at the lower part of the adult range (see Table 10-1). One of the adult females contained one embryo in the left oviduct and two in the right oviduct, measuring 5 mm crown to rump length. Mammary formula: 1-0-2 (n = 2).

REMARKS—In the 1260 m elevational zone, one individual of this species was captured in a Sherman trap placed on the ground at a hole under tree roots. *Microgale gymnorhyncha* is known from three localities, the RNI d'Andringitra (the type locality), Fanovana (Jenkins et al., 1996), and the RS d'Anjanaharibe-Sud.

Microgale monticola, new species

HOLOTYPE—FMNH 154012 (field number SMG 7020), adult female, skin and skull, collected 15 November 1994 by Steven M. Goodman.

TYPE LOCALITY—11 km WSW of Befingitra, Réserve Spéciale d'Anjanaharibe-Sud, 14°44'S, 49°26'E, 1550 m.

PARATYPES—FMNH 154013, 154014, 154227: 11 km WSW of Befingitra, 14°44'S, 49°26'E, 1550 m; FMNH 154019, 154228, 154229: 12.2 km WSW of Befingitra, 14°44'S, 49°26'E, 1950 m.

DISTRIBUTION—Recorded to date only from the RS d'Anjanaharibe-Sud.

HABITAT—Collected in montane and upper montane forest, at an altitude of 1550–1950 m on wet ground in valley bottoms, on slopes dominated by bamboo, and on ridge crests.

DIAGNOSIS—Similar in size to *Microgale thomasi* but with tail longer than head and body. Pelage dark dorsally and ventrally. Skull moderately robust, interorbital region broad with frontals slightly dorsolaterally inflated. Upper and lower canines robust, upper and lower first premolars (P2 and p2) large; P2 with well-developed anterior and posterior accessory cusps, p2 anteroflexed.

DESCRIPTION—Moderately robust, medium-sized species of *Microgale* with tail longer than head and body (see Fig. 10-2, Tables 10-1, 10-2). Dorsal pelage dark brown and slightly grizzled; hairs with silvery gray bases, tops banded dark brown, then red-brown with dark brown tips; guard hairs with gray bases and long, dark brown tops. Ventral pelage dark brown; individual hairs with silvery gray bases but tops of some banded buff, then brown with buff tips, others with brown tops; guard hairs with gray bases and buff tops. Tail dark brown dorsally, paler ventrally; tail scale hairs sparse and short, approximately 1.5 mm scales in length, so scales are clearly visible. Feet dark brown. Forefeet moderately long and broad with well spaced cheiridia and moderately long claws; digits slightly lengthened. Hindfoot long with slightly elongated, well spaced cheiridia, slightly lengthened digits, heel naked with sparse, short hairs on lateral margins. The digits of fore- and hindfeet are similar in proportions, with the first digit reaching just beyond the base of the second and the fifth reaching the distal joint of the fourth digit. Skull moderately large (see Tables 10-1, 10-2, Fig. 10-3), rostrum moderately elongated, nasals terminate dorsal to the zygomatic plate, interorbital region broad with frontals slightly dorsolaterally inflated, parietals moderately large, braincase rounded, moderately broad, and deep, tapering slightly from anterior to posterior, supraoccipital crest absent; palate with posterior incisive foramina lying between I3, linked
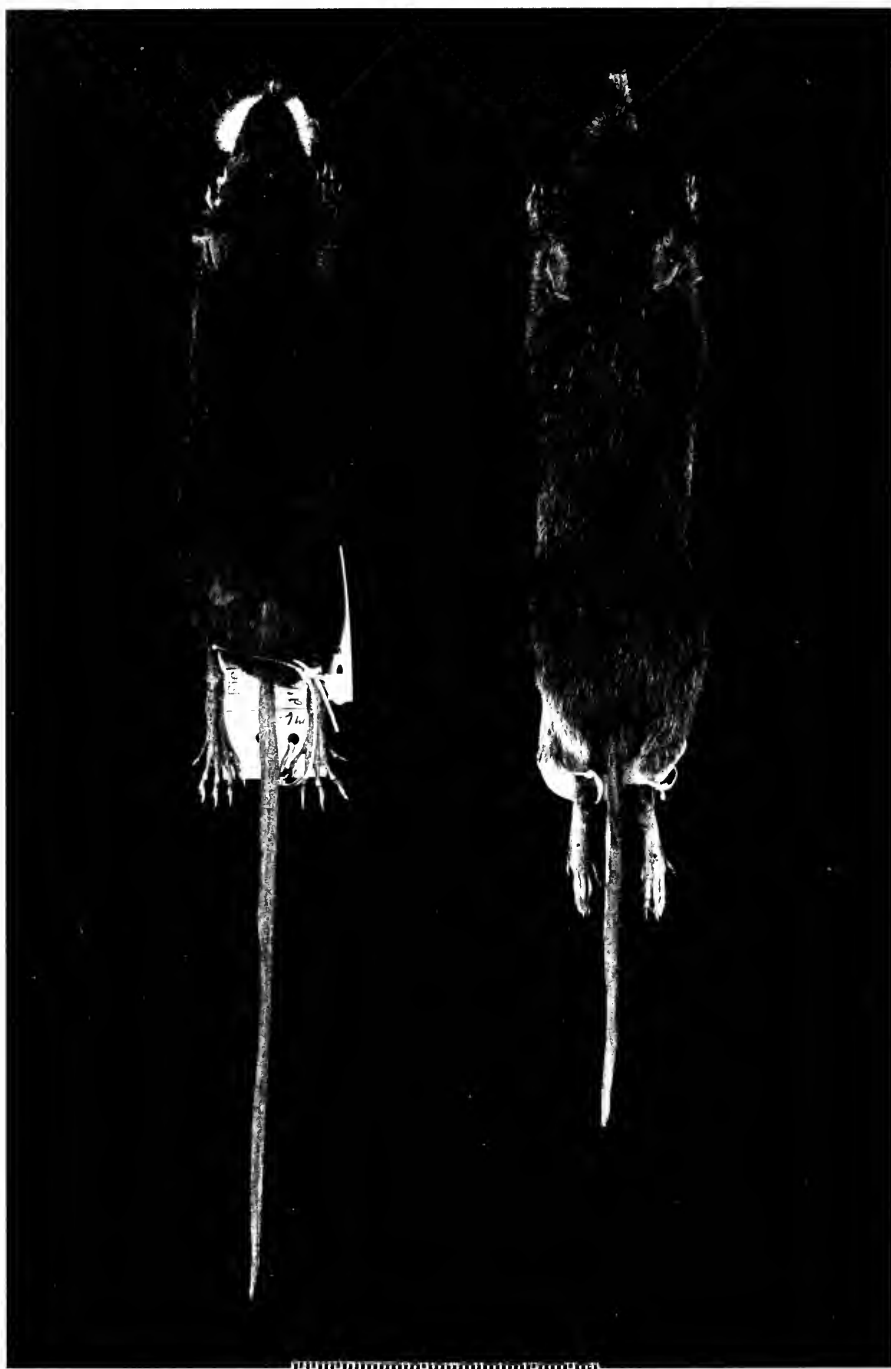
FIG. 2.   Dorsal view of skins of *Microgale monticola* (FMNH 154012) (**left**) and *M. thomasi* (BM(NH) 97.9.1.108) (**right**). Scale = 1 mm.

Character	Microgale monticola	Microgale thomasi	Microgale soricoides
Head and body length	81–92 85.8 ± 4.35 (5)	91–97 93.7 ± 2.49 (3)	85–103 90.4 ± 6.8 (5)
Tail length	105–113 109.5 ± 2.43 (6)	62–72 66 ± 4.3 (3)	84–97 92.6 ± 4.63 (5)
Ratio of tail length to head and body length	1.2–1.4 1.3 ± 0.07 (4)	0.7–0.8 0.7 ± 0.05 (3)	0.9–1.1 1.0 ± 0.07 (4)
Ratio of tail length to condyloincisive length	4.1–4.4 4.3 ± 0.10 (5)	2.4–2.7 2.5 ± 0.14 (3)	3.3–3.7 3.6 ± 0.16 (4)
Hindfoot length	20–21 20.8 ± 0.37 (6)	18.7–19 18.9 ± 0.14 (3)	17–18 17.4 ± 0.49 (5)
Condyloincisive length	25.5–25.8 25.7 ± 0.12 (5)	25.9–27.1 26.5 ± 0.51 (4)	25.5–26.3 25.9 ± 0.29 (4)
Braincase breadth	10.5–11.1 10.9 ± 0.21 (5)	11.2–11.6 11.4 ± 0.15 (4)	10.6–11.1 11.0 ± 0.22 (4)
Mandible length	17.3–17.5 17.4 ± 0.08 (5)	17.9–19.2 18.6 ± 0.52 (4)	17.0–17.3 17.2 ± 0.12 (4)
Mandible height at coronoid process	5.3–5.6 5.5 ± 0.1 (5)	6.0–6.5 6.3 ± 0.19 (4)	6.4–7.2 6.8 ± 0.29 (4)
Ascending ramus length	5.7 ± 6.0 5.8 ± 0.10 (5)	6.2–6.9 6.7 ± 0.29 (4)	6.0–6.6 6.3 ± 0.22 (4)

* Measurements are given as the range, followed by the mean ± SD and sample size (in parentheses).

to anterior incisive foramina by short commissures; posterior border of palatine broad and slightly curved, mesopterygoid anteriorly broad, tapering posteriorly (see Fig. 10-3), pterygoids narrow anteriorly, broader in midline, outer lateral margin curved. Mandible moderately robust, slightly sinuous, mental foramen lies below posterior root of p2 or between p2 and p3. Dentition (see Fig. 10-4) with short diastemata between anterior teeth from I1 to P2 or P3 and usually on either side of p2. First two upper incisors (I1, I2) with prominent distostyles, a small distostyle is present on third upper incisor (I3) and also canine (C), anterior accessory cusps may also be present on I2 and C; first upper premolar (P2) robust, double rooted with small, well marked anterior and posterior accessory cusps, and a distinct lingual cingulum with a small anterolingual cuspid is present; diastemata usually present between all of the anterior teeth from I1 to P3; anterior ectostyle

of second upper premolar (P3) present but poorly differentiated from paracone, distostyle not differentiated; third upper premolar (P4) with prominent mesostyle and anterior ectostyle, distostyle present but poorly differentiated; upper molars as for the genus. Lower incisors as for the genus, with well-developed posterior cusps; no anterior cuspid on canine (c) but anterolingual cingulum present; first lower premolar (p2) robust, anteroflexed, tricuspid, double rooted, very similar in form and only slightly smaller than second lower premolar (p3); third lower premolar (p4) with a small cuspid on talonid; lower molars as for genus; hypoconid of third lower molar (m3) low, entoconid ridge present, entoconid absent, talonid basin present, narrow.

DECIDUOUS DENTITION—This is based on a single individual in which the deciduous dentition is not fully erupted. Deciduous upper and lower incisors, canines and premolars are similar to the
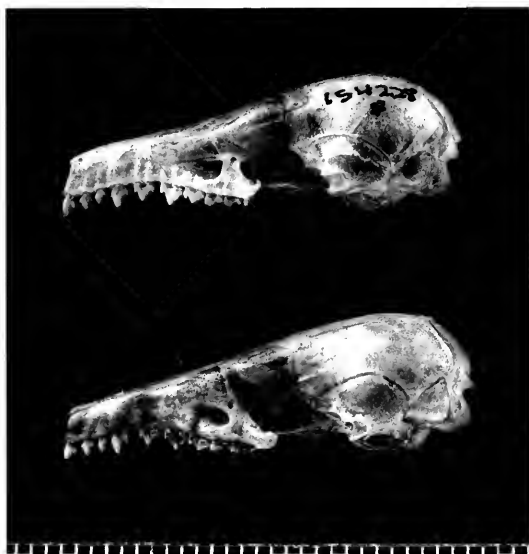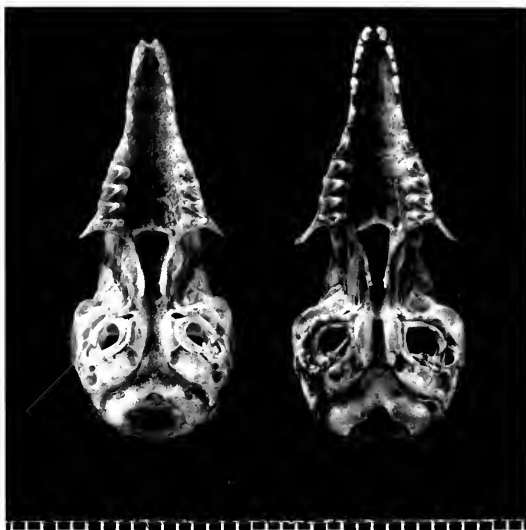
Fig. 3. Crania of *Microgale monticola* (FMNH 154228) and *M. thomasi* (BM(NH) 95.R26). Upper sets of photographs of *M. monticola* and *M. thomasi* (left to right) of dorsal and ventral views. Scale = 1 mm. Lower sets of photographs of *M. monticola* (top) and *M. thomasi* (lower) of left lateral views of skulls and mandibles. Scale = 1 mm.

permanent teeth but smaller; slight trace of metaconid on dp3. Because no juveniles were collected, no comments on the eruption sequence are possible.

ETYMOLOGY—The name of the new species, *monticola*, Latin for "of the mountain," is derived from the montane habitat in which it occurs.

COMPARISONS—In comparison with other species of *Microgale* collected from RS d'Anjanaharibe-Sud, *M. monticola* is larger than

M. parvula and *M. longicaudata*, averages larger than *M. cowani* and *M. principula*, but is smaller than *M. gymnorhyncha*, *M. dobsoni*, and *M. talazaci* (see Table 10-1). *Microgale monticola* differs from *M. cowani* in its greater tail length relative to that of head and body (ratio 0.7–0.9, mean 0.8 ± 0.07, n = 7 in *M. cowani*; ratio 1.2–1.4, mean 1.3 ± 0.07, n = 5 in *M. monticola*), longer hindfoot, and larger skull. It is readily distinguished from *M. principula*, which has an ex-
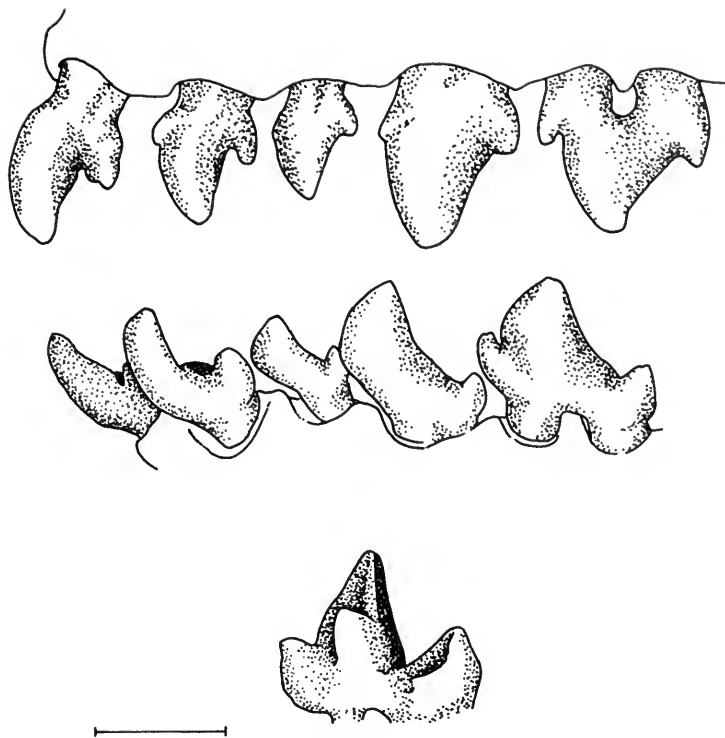
Fig. 4. Dentition of *Microgale monticola* (FMNH 154012). Buccal view of left I1–P2 (**top**), buccal view of left i1–p2 (**middle**), and lingual view of right m3 (**bottom**). Scale = 1 mm.

tremely long tail approximately twice as long as head and body length (ratio of tail to head and body length 2.1 in the subadult (FMNH 154004), (1.9 in the juvenile (FMNH 154003) *M. principula*). *Microgale monticola* is similar in body and cranial size to *M. soricoides*, although it averages slightly smaller (see Tables 10-1, 10-2); the two species are, however, discernable externally by the paler, buffy gray, more speckled dorsal pelage, reddish buff wash on the venter, and paler feet of *M. soricoides* and the longer hindfeet and greater relative tail length of *M. monticola*. In craniodental features these two species are readily distinguished. Cranially *M. monticola* is separated from *M. soricoides* by the slightly narrower rostrum (2.9–3.2; mean 3.1 ± 0.10, n = 5 in *M. monticola*; 3.2–3.8, mean 3.5 ± 0.22, n = 4 in *M. soricoides*), deeper occiput (3.4–3.9, mean 3.8 ± 0.21, n = 4 in *M. soricoides*; 4.5–4.7, mean 4.6 ± 0.08, n = 5 in *M. monticola*), and less robust mandible (see Table 10-2). The two species are dentally distinguished by the characteristically robust first upper and lower incisors and small, single-rooted upper and lower first premolars of *M. soricoides* in comparison with the unmodified up-

per and lower first incisors and large, double-rooted first premolars of *M. monticola*.

Of those species of *Microgale* recorded from elsewhere in Madagascar, *M. monticola* is easily distinguished on the basis of size and morphology, with the exception of *M. thomasi* (Major, 1896a), a species poorly represented in museum collections, so far recorded mostly from more southerly localities in the eastern rain forest. These two species are similar in body size and dental features (see Table 10-2, Figs. 10-2, 10-3). *Microgale thomasi* is paler, more rufous, and more speckled in dorsal coloration than *M. monticola*, with the venter distinctly paler than the dorsum and with a more definitely bicolored tail. *Microgale thomasi* is slightly larger and more robust in appearance, with the tail shorter than the head and body length and with shorter hindfeet, whereas *M. monticola* is readily distinguished by its long tail relative to the head and body length and longer hindfeet; the tail of *M. thomasi* has moderately long, dense scale hairs, particularly proximally, unlike the short scale hairs of *M. monticola*. In *M. monticola* the digits of the hindfeet are slightly elongated, with the first digit

reaching beyond the basal phalange of the second digit, and the fifth digit reaching the base of the distal phalange of the fourth digit; the cheiridia are elongated and well spaced; the sole is naked apart from sparse, short hairs on the lateral margin of the tarsus. In contrast, the digits of *M. thomasi* are not elongated, the first digit barely reaches the first phalange of the second digit, the fifth digit only midway along the second phalange of the fourth digit; the cheiridia are rounded and closely grouped; the sole is clothed with short hairs. The cranial dimensions and morphology of the facial region of the crania of both species are very similar with greater differences evident in the posterior regions of the crania. The commissures linking the anterior and posterior incisive foramina are short and poorly defined, and the posterior incisive foramina are positioned between the third upper incisors in *M. monticola*, whereas in *M. thomasi*, the posterior incisive foramina lie between the posterior part of the canines and are linked to the anterior foramina via longer, well-defined commissures. In contrast to the morphology of the pterygoid region of *M. monticola*, in *M. thomasi* the posterior border of the palatine is narrow and rounded, the mesopterygoid region tapers only slightly from anterior to posterior, the pterygoid region is longer, and the outer lateral margin is more or less straight (see Fig. 10-3) (length of pterygoid region from posterior border of the palate to inferior articular facet 4.4–4.7, mean 4.6 ± 0.12, n = 5 in *M. monticola*; 5.1–5.6, mean 5.4 ± 0.21, n = 4 in *M. thomasi*). The basisphenoid is stepped between the anterior region of the tympanic bullae in *M. thomasi* but level in *M. monticola*. In dorsal view the shape of the braincase differs in the two species; that of *M. thomasi* is shorter, broader anteriorly and tapers more abruptly posteriorly, the parietal is noticeably shorter in the midline (parietal length 4.4–4.9, mean 4.6 ± 0.19, n = 4 in *M. thomasi*; 5.9–6.4, mean 6.1 ± 0.17, n = 5 in *M. monticola*), the parietal-occipital suture is more dorsally positioned, and a supraoccipital crest is present, unlike *M. monticola*. The mandible of *M. thomasi* is larger and more robust than that of *M. monticola*. There are few differences in the dentition of these two species, both of which have unusually large upper and lower first premolars (a character previously considered to be diagnostic of *M. thomasi*), except that p4 is trenchant in *M. thomasi* but anteroflexed in *M. monticola*; the hypoconid of m3 is prominent in *M. thomasi* but low in *M. monticola*, which also differs in having a narrower

talonid basin. In the single specimens of each species in which the dentition is deciduous, there is a trace of an anterior cuspid on di3 in *M. thomasi*, which is absent in *M. monticola*, whereas a metaconid is well developed on dp3 in *M. thomasi* but reduced to a trace in *M. monticola*.

MEASUREMENTS—External and cranial measurements are presented in Table 10-1.

VARIATION—There is no evidence of substantial variation within this small sample.

POPULATION STRUCTURE AND REPRODUCTION—The sample contained six adults with a male-to-female ratio of 1:5, plus a single infant with the deciduous dentition still erupting. The adult male had testes measuring 5 × 5 mm with convoluted epididymides. One of the adult females contained a single embryo in the right oviduct measuring 6 mm in crown to rump length. Mammary formula: 1-0-2 (n = 4); 0-1-2 (n = 1).

REMARKS—At 1550 m elevation, a specimen of *Microgale monticola* was captured in a Sherman trap placed on the ground at the opening of a cavity in the roots of a small tree.

Ecological Analysis

General

A total of 1,045 pitfall bucket-days was accrued during the small mammal survey of the eastern slopes of the RS d'Anjanaharibe-Sud, between 19 October and 30 November 1994, comprising 319 bucket-days at 875 m, 264 at 1260 m, 231 at 1550 m, and 231 at 1950 m (Table 10-3). Seventy-four small mammals were captured, including 68 *Microgale*, four *Setifer*, and two *Gymnuromys roberti* (Major, 1896a) (for rodents, see Chapter 12). Furthermore, 2,550 trap-nights using small mammal traps were also accrued (Chapter 12), and 13 (0.51%) Tenrecidae were captured. All species of *Microgale* recorded during the survey were captured in the pitfall traps, and five species of *Microgale* (*M. longicaudata, M. monticola, M. gymnorhyncha, M. dobsoni,* and *M. talazaci*) as well as *Setifer* were also trapped in standard live mammal traps. At 1550 m, seven species of *Microgale* were captured, two of which (*M. longicaudata* and *M. talazaci*) were trapped only in standard live traps. In the other three elevational zones, the species taken in live traps comprised a subset of those obtained in pitfall traps.

The combined trapping results, with pitfall and

TABLE 10-3. Characteristics and capture results of small mammals obtained in all pitfall lines.

Character	Line 1	2	3	4	5	6	7	8	9	10	11	12
Descriptive information												
Forest type	Lowland 875 m			Montane 1260 m			Upper montane 1550 m			Upper montane 1950 m		
Altitude, m	890	850	850	1250	1230	1240	1550	1510	1500	1970	1930	1950
Line placement*	R	V	S	R	V	S	R	V	S	R	V	S
First sample day (day/month)	19/10	19/10	20/10	4/11	4/11	4/11	15/11	15/11	15/11	24/11	24/11	24/11
Last sample day (day/month)	28/10	28/10	28/10	10/11	10/11	10/11	21/11	21/11	21/11	30/11	30/11	30/11
Total trap-days	110	110	99	88	88	88	77	77	77	77	77	77
Species sampled												
Mammalia												
Setifer setosus	2		2									
Microgale cowani					4		3	6	4	2	3	4
Microgale longicaudata				1	1					1		1
Microgale principula	3					2		1			1	1
Microgale parvula				4	3	1						
Microgale dobsoni				1								
Microgale talazaci				3	3							
Microgale soricoides						2		1				
Microgale gymnorhyncha					1			2	1			
Microgale monticola								2	2	2	1	
Gymnuromys roberti					1	1						
Mammal capture results												
Total number of captures	5	0	2	9	13	6	3	12	7	5	5	6
Total number of species	2	0	1	4	6	4	1	5	3	3	3	3
Capture success, %	4.5	0.0	2.0	10.2	14.8	6.8	3.9	15.6	9.1	6.5	6.5	7.8
Total number of *Microgale* captured	3	0	0	9	12	5	3	12	7	5	5	6
Total number of *Microgale* species	1	0	0	4	5	3	1	5	3	3	3	3
Microgale capture success, %	2.7	0.0	0.0	10.2	13.6	5.7	3.9	15.6	9.1	6.5	6.5	7.8

* R = ridge; S = slope; and V = valley.

standard live traps, include 10 species of Tenrecidae (*Setifer* and nine species of *Microgale*). None of the *Microgale* had been recorded previously in the reserve, and one is proposed herein as new to science. Before proceeding with the analysis of the trapping results, it is important to determine whether the sampling effort was sufficient to reflect some measure of completeness for the survey and the actual tenrecid species richness within each elevational zone.

Species Accumulation Curves

By plotting the total number of species known from each pitfall line (11 pitfall buckets per 24 hr period) or elevational zone (33 pitfall buckets per 24 hr period), species accumulation curves may be drawn. An examination of these curves (Fig. 10-5) shows that no additional species of *Microgale* was added in the 875 m zone after 66 pitfall bucket-days (total, two species in 319 pitfall bucket-days), in the 1260 m zone after 165 pitfall bucket-days (total, seven species in 264 pitfall bucket-days), in the 1550 m zone after 198 pitfall bucket-days (total, five species in 231 pitfall bucket-days; two other species only in standard live traps), and in the 1625 m zone after 99 pitfall bucket-days (total, four species in 231 pitfall bucket-days). The flattening of the species accumulation curve within each elevational zone with additional trapping effort did not generally coincide with a general decline in overall pitfall trap success (Fig. 10-5). However, the number of insectivores captured in each elevational zone tended to decline during the time that the lines were in place.

Trapping Success and Abundance

The results of the pitfall trapping are presented in Table 10-3. In each elevational zone, three pitfall lines were in use for a minimum of 7 days, and there was considerable variation in the capture rate of insectivores within and between the lines. For *Microgale* at 875 m, the capture success rate for the three lines varied from 0 to 2.7%; at 1250 m, from 6.8 to 13.6%; at 1550 m, from 3.9 to 15.6%; and at 1950 m, from 6.5 to 7.8%.

One important question concerns our sampling protocol: Do trapping results reflect the relative abundance of the various *Microgale* in the reserve during the survey? A response is not simple.
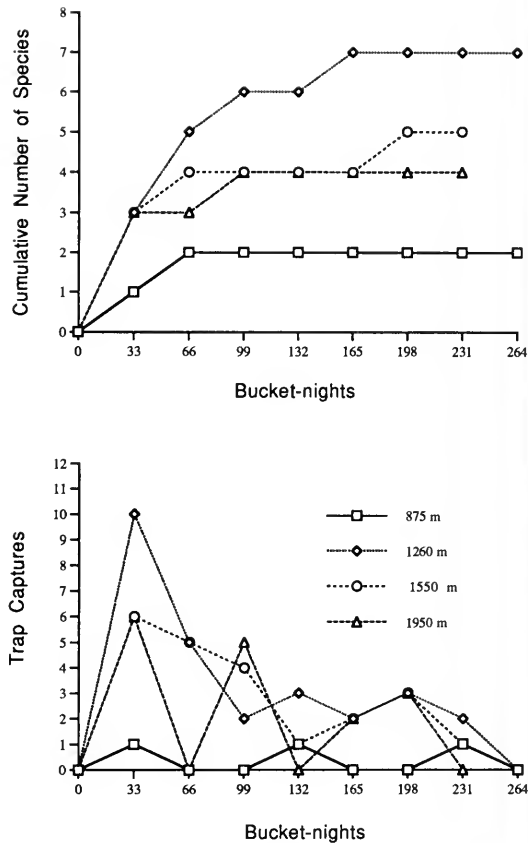
FIG. 5. Species accumulation curves (**top**) and pitfall trap success (**bottom**) plotted for each elevational zone against the total number of bucket-nights. Information from the three lines in each zone is combined.

However, because the lines were placed randomly in a variety of microhabitats within each elevational zone, because partially arboreal species are regularly captured in the pitfall buckets and we have no evidence of strictly arboreal tenrecs, and because our species-accumulation curves generally reached an asymptote after a few days and further trapping efforts generally did not result in additional new species to the elevational list, we believe that our results are a good first approximation of relative species richness and general abundance of small insectivores within the reserve during the season of our study. Furthermore, other studies of Malagasy insectivores using pitfall traps indicate that this technique is most efficient for documenting species richness in eastern humid forest (Raxworthy & Nussbaum, 1994; Goodman et al., 1996).

Relationship between Abiotic Factors and Insectivore Capture Rates

Information was gathered in the RS d'Anjanaharibe-Sud at each site on daily minimum and maximum temperatures as well as precipitation (see Chapter 1). To determine whether Insectivora capture rates, particularly *Microgale*, were influenced by these climatic factors, a series of nonparametric Kendall's rank correlations were made. In these, the Y variable was the number of animals captured, and the X variable was the minimum temperature the morning the line was checked, the maximum temperature the previous afternoon, and the amount of precipitation during the previous 24 and 48 hr periods. In no case was any of these variables correlated to insectivore trap success.

Species Diversity

On the basis of our trapping results, there is a clear indication of variation in the elevational ranges of many of the tenrecs on the slopes of the reserve. A total of 10 Insectivora (*Setifer* and nine *Microgale* species) were captured during the 1994 survey of the reserve using two trapping techniques, pitfall and standard live traps. No evidence of the two Soricidae, *Suncus madagascariensis* or the introduced *Suncus murinus*, was found in the reserve.

The number of Tenrecidae known in each elevational zone (with the number of *Microgale* in parentheses) is as follows: 875 m, three (one); 1260 m, eight (seven); 1550 m, seven (seven); and 1950 m, four (four) species (Table 10-4). Thus, for the genus *Microgale*, there appears to be a midelevational peak in species richness between 1260 and 1550 m. A parallel pattern was found in the RNI d'Andringitra (Goodman et al., 1996).

No species of Insectivora was found across the breadth of the elevational transect. This is in contrast to the RNI d'Andringitra, where two species (*Microgale taiva* and *M. parvula*), and probably a third species (*M. longicaudata*), occurred across the complete elevational transect between 720 and 1625 m (Goodman et al., 1996). On the basis of our trapping results in the RS d'Anjanaharibe-Sud, two tenrecs (*Setifer* and *M. principula*) are confined to lowland forests at 875 m, and one (*M. dobsoni*) is confined to montane forest at 1260 m. The other species of *Microgale* have relatively

TABLE 10-4. Known elevational distribution of Tenrecidae on the eastern slopes of the RS d'Anjanaharibe-Sud.*

Species	Elevational range			
	875 m	1260 m	1550 m	1950 m
Setifer setosus	+	–	–	–
Tenrec ecaudatus	(+)	(+)	–	–
Microgale cowani	–	+	+	+
Microgale longicaudata	–	+	+	+
Microgale principula	+	–	–	–
Microgale parvula	–	+	+	+
Microgale dobsoni	–	+	–	–
Microgale talazaci	–	+	+	–
Microgale soricoides	–	+	+	–
Microgale gymnorhyncha	–	+	+	–
Microgale monticola	–	–	+	+
Total number of Insectivora	3	8	7	4
Total number of *Microgale* spp.	1	7	7	4
Microgale spp. in each zone, %	10	70	70	40

* Includes sight records (in parentheses) and records of species obtained in live traps and pitfall traps from the 1994 survey.

broad distributions in the montane and upper montane forest zones.

In general our measures of *Microgale* species richness in each elevational zone parallel total capture rates. Thus, the greatest pitfall capture rates were at 1260 m (27 individuals) and 1550 m (22 individuals), followed by 1950 m (16 individuals) and finally 875 m (three individuals) (Table 10-3). The single exception was *M. cowani*, which did not follow this pattern; it was most common at 1550 m (13 individuals), followed by 1950 m (nine individuals), then 1260 m (four individuals).

Habitat Separation

Within each elevational zone pitfall lines were installed in three different habitats: ridges, valley bottoms, and on hill or slope crests. An analysis of the pitfall trapping results segregated by these habitat variables allows us to speculate on possible differences in microhabitat utilization by different species of *Microgale*. Of the 68 *Microgale* trapped in pitfall buckets, 20 were obtained on ridges, 30 in valleys, and 17 on slopes (Table 10-3). Although these differences are not statistically significant, there appears to be a tendency for

more individuals of this genus to occur in valley bottoms. Furthermore, a total of seven species were captured on ridges, eight in valley bottoms, and six on slopes (Table 10-5). Thus, in general, relative density and species richness appear to be highest in valleys, followed by ridges, and lowest on slopes. In the RNI d'Andringitra, the highest density of soil invertebrates was likewise found in valleys, followed by ridges, and finally slopes (Goodman et al., 1996). When analyzed by species, the same general pattern exists for some taxa, but within elevational zones there is considerable variation (Table 10-5). In all elevational zones, M. cowani was more common in valleys than the other microhabitats, the only exception being at 1950 m, where 33% were taken in valleys as compared with 44% on slopes. Microgale gymnorhyncha and M. monticola were also more common in valleys than the other two microhabitats, whereas species such as M. principula and M. dobsoni were exclusively or generally trapped on slopes. Microgale longicaudata was evenly distributed between ridges and valleys.

Ecological Separation

On the basis of their very long tail with a prehensile tip, elongated hindfoot, and similar dentition, M. longicaudata and M. principula are either closely related within the Microgale clade or ecological counterparts of one another. It is now known that M. longicaudata is partially arboreal, as is presumably M. principula. To our knowledge, the co-occurrence of these two species observed on the slopes of the RS d'Anjanaharibe-Sud is the first record of these species in the same forest. Interestingly enough, they were not found in direct sympatry, but rather M. principula was only in the 875 m zone, and M. longicaudata occurred higher on the mountain.

A parallel case of morphological similarity may be made for Microgale talazaci and M. dobsoni, particularly in body size, tail proportions, and cranial and dental structure. In this case, however, they partially overlapped in elevational range; the former species was found in the 1260 and 1550 m zones, and the latter only at 1260 m.

The variation in morphology of the other species of Microgale collected from RS d'Anjanaharibe-Sud suggests some ecological separation. The very small size of M. parvula implies a distinct life strategy; the specialized dentition, modified rhinarium, and broad forefeet of M. gymnor-

TABLE 10-5. Microhabitat differences in the occurrence of Microgale on the slopes of the RS d'Anjanaharibe-Sud.*

Species	875 m R	875 m V	875 m S	1260 m R	1260 m V	1260 m S	1550 m R	1550 m V	1550 m S	1950 m R	1950 m V	1950 m S	Combined R	Combined V	Combined S
Microgale cowani					100		23	46	31	22	33	44	19	50	31
Microgale longicaudata				50	50					50	50		50	40	50
Microgale principula	100												100		
Microgale parvula				50	38	100							50	38	60
Microgale dobsoni				25	75	13							25	75	13
Microgale talazaci				60		40		100					50	17	33
Microgale soricoides					100						50			75	25
Microgale gymnorhyncha				33			66	66	50	66	33		28	29	43
Microgale monticola							33	50	33	33	33	33	29	38	33
Total Microgale captures, %	100	0	0		42	25	11	56	33		33	33		38	33
Number of Microgale spp.	1	0	0	4	5	3	1	5	3	3	3	3	6	8	7

* Figures presented as the percent capture (rounded) of Microgale species within each elevational zone.

† R = ridge; S = slope; and V = valley.

hyncha suggest a considerable difference in ecology (possibly ground dwelling and conceivably semifossorial) from that of *M. soricoides*, with its slender feet (possibly more scansorial) and equally specialized but different dentition. The other two species with an apparently unspecialized dentition and body form, *M. cowani* and *M. monticola*, nevertheless differ in external size and proportions and, presumably, lifestyle.

Discussion

In general, the vast majority of *Microgale* species expected to occur within the reserve on the basis of their known distribution in the northern portion of the eastern humid forests were captured during the 1994 biological inventory of the RS d'Anjanaharibe-Sud. There are a few notable exceptions that warrant some discussion here.

Microgale drouhardi (Grandidier, 1934), including *M. melanorrhachis* (Morrison-Scott, 1948; see Jenkins et al., 1997), is a widespread species known from areas north of the RS d'Anjanaharibe-Sud (PN de la Montagne d'Ambre) and south to the RNI d'Andringitra. However, this species has a patchy distribution and generally is locally common. Thus, the absence of this species from our samples taken in the RS d'Anjanaharibe-Sud probably reflects its actual absence from the reserve. Two other *Microgale* are known from the eastern humid forest yet were not captured in the RS d'Anjanaharibe-Sud, *M. thomasi* (Major, 1896a), a species rare in collections and recorded mainly from areas farther south in the eastern humid forest, and *M. pusilla*, another species with apparently widely disjunct populations and a patchy distribution (MacPhee, 1987). The absence of the latter species is surprising in view of its documented presence in the nearby RNI de Marojejy (Nicoll & Langrand, 1989).

Within the endemic Insectivora there are a few other distributional anomalies. During our inventory of the reserve, we found no evidence of *Hemicentetes* (Mivart, 1871) or *Oryzorictes* (Grandidier, 1870). However, during a survey of the western slopes of the RS d'Anjanaharibe-Sud conducted by Franco Andreone between 25 February and 12 February 1996 within the elevational range of 1000–1300 m, *Hemicentetes* was observed and photographed, and *Oryzorictes talpoides* G. Grandidier & Petit, 1930, *Microgale taiva*

(Major, 1896b), and *M. fotsifotsy* Jenkins et al., 1997 were captured using pitfall techniques. The vegetation of the western slopes of the reserve is similar to that of the eastern slopes, although the former may receive less annual precipitation. It is not clear whether these species occur on the eastern slopes of the reserve and were overlooked during the 1994 survey. Furthermore, no *Tenrec ecaudatus* was captured during the 1994 inventory, although several individuals were observed at night in the 875 and 1260 m altitudinal zones. Another interesting record is that of *M. dryas* (Jenkins, 1992), which is based on the fragments of a skull (probably a single juvenile specimen) included in a *Tyto soumagnei* (Madagascar Red Owl) pellet collected at the edge of the reserve at Antsahamifelana (14°46′S, 49°28′E). Combining all sources of information, 16 species of Insectivora have been recorded within the reserve, 12 of which belong to the genus *Microgale*.

On the basis of the species-accumulation curves for each elevational zone and extrapolation of what should presumably occur in the reserve and what was found, we conclude that the Insectivora fauna, particularly species of *Microgale*, on the eastern slopes of the RS d'Anjanaharibe-Sud has been thoroughly, although not completely, surveyed.

Acknowledgments

Literature Cited

Butler, P. M., and M. Greenwood. 1979. Soricidae (Mammalia) from the Olduvai Gorge, Tanzania. Zoological Journal of the Linnean Society, **67**: 329–379.

Carleton, M., and D. F. Schmidt. 1990. Systematic

studies of Madagascar's endemic rodents (Muroidea: Nesomyinae): An annotated gazetteer of collecting localities of known forms. American Museum Novitates, **2987**: 1–36.

COQUEREL, C. 1848. Note sur une espèce nouvelle de musaraigne trouvée à Madagascar. Annales des Sciences Naturelles, Zoologie, **9**: 193–198.

CUVIER, G. 1798. Tableau élémentaire de l'histoire naturelle des animaux. Paris.

DOBSON, G. E. 1882. A monograph of the Insectivora, systematic and anatomical. Part 1, including the families Erinaceidae, Centetidae and Solenodontidae. John van Voorst, London, 172 pp., 23 pls.

EISENBERG, J. F., AND E. GOULD. 1970. The tenrecs: A study in mammalian behavior and evolution. Smithsonian Contributions to Zoology, **27**: 1–138.

GOODMAN, S. M., C. J. RAXWORTHY, AND P. D. JENKINS. 1996. Insectivore ecology in the Réserve Naturelle Intégrale d'Andringitra, Madagascar, pp. 218–230. *In* Goodman, S. M., ed., A floral and faunal inventory of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: With reference to elevational variation. Fieldiana: Zoology, n.s., **85**: 1–319.

GRANDIDIER, A. 1870. Description de quelques animaux nouveaux, découverts à Madagascar. Revue et Magasin de Zoologie, **22**: 49–54.

GRANDIDIER, G. 1934. Deux nouveaux mammifères insectivores de Madagascar. Bulletin de Muséum National d'Histoire Naturelle, série 2, **6**: 474–477.

GRANDIDIER, G., AND G. PETIT. 1930. Description d'une espèce nouvelle d'Insectivore Malgache, suivie de remarques critiques sur le genre *Oryzoryctes*. Bulletin du Muséum National d'Histoire Naturelle, série 2, **2**: 498–505.

JENKINS, P. D. 1988. A new species of *Microgale* (Insectivora: Tenrecidae) from northeastern Madagascar. American Museum Novitates, **2910**: 1–7.

———. 1992. Description of a new species of *Microgale* (Insectivora: Tenrecidae) from eastern Madagascar. Bulletin of the British Museum Natural History (Zoology), **58**: 53–59.

———. 1993. A new species of *Microgale* (Insectivora: Tenrecidae) from Eastern Madagascar with an unusual dentition. American Museum Novitates, **3067**: 1–11.

JENKINS, P. D., S. M. GOODMAN, AND C. J. RAXWORTHY. 1996. The shrew tenrecs (*Microgale*) (Insectivora: Tenrecidae) of the Réserve Naturelle Intégrale d'Andringitra, Madagascar, pp. 191–217. *In* Goodman, S. M., ed., A floral and faunal inventory of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: With reference to elevational variation. Fieldiana: Zoology, n.s., **85**: 1–319.

JENKINS, P. D., C. J. RAXWORTHY, AND R. A. NUSSBAUM. 1997. A new species of *Microgale* (Insectivora, Tenrecidae), with comments on the status of four other taxa of shrew tenrecs. Bulletin of the British Museum Natural History (Zoology), **63**: 1–12.

LINNAEUS, C. 1766. Systema Naturae per Regna Tria Naturae Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis, 12th edition. Holmiae.

MACPHEE, R. D. E. 1987. The shrew tenrecs of Mada-gascar: Systematic revision and Holocene distribution of *Microgale* (Tenrecidae, Insectivora). American Museum Novitates, **2889**: 1–45.

MAJOR, C. I. FORSYTH. 1896a. Diagnoses of new mammals from Madagascar. Annals and Magazine of Natural History, series 6, **18**: 318–325.

———. 1896b. Descriptions of four additional new mammals from Madagascar. Annals and Magazine of Natural History, series 6, **18**: 461–463.

MILLS, J. R. E. 1966. The functional occlusion of the teeth of Insectivora. Journal of the Linnean Society (Zoology), **47**: 1–125.

MIVART, G. 1871. On *Hemicentetes*, a new genus of Insectivora, with some additional remarks on the osteology of that Order. Proceedings of the Zoological Society of London, **1871**: 58–79.

MORRISON-SCOTT, T. C. S. 1948. The insectivorous genera *Microgale* and *Nesogale* (Madagascar). Proceedings of the Zoological Society of London, **118**: 817–822.

NICOLL, M. E., AND O. LANGRAND. 1989. Madagascar: Revue de la conservation et des aires protégées. World Wide Fund for Nature, Gland, Switzerland, xvii + 374 pp.

RAND, A. L. 1936. The distribution and habits of Madagascar birds: A summary of the field notes of the Mission Zoologique Franco-Anglo-Américaine à Madagascar. Bulletin of the American Museum of Natural History, **72**: 143–499.

RAXWORTHY, C. J., AND R. A. NUSSBAUM. 1994. A rainforest survey of amphibians, reptiles and small mammals at Montagne d'Ambre, Madagascar. Biological Conservation, **69**: 65–73.

———. 1996. Amphibians and reptiles of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: A study of elevational distribution and local endemicity, pp. 158–170. *In* Goodman, S. M., ed., A floral and faunal inventory of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: With reference to elevational variation. Fieldiana: Zoology, n.s., **85**: 1–319.

RAXWORTHY, C. R., J.-B. RAMANAMANJATO, AND A. RASELIMANANA. 1994. Les reptiles et les amphibians, pp. 41–57. *In* Goodman, S. M., and O. Langrand, eds., Inventaire Biologique Forêt de Zombitse. Recherches pour le Developpement, Série Sciences biologiques, No. Spécial. Centre d'Information et de Documentation Scientifique et Technique, Antananarivo, Madagascar, 106 pp.

SCHREBER, J. C. D. VON. 1777. Die Säugethiere in Abbildungen nach der Natur mit Beschreibungen, volume 3. Leipzig.

STEPHENSON, P. J. 1994. Seasonality effects on small mammal trap success in Madagascar. Journal of Tropical Ecology, **10**: 439–444.

———. 1995. Taxonomy of shrew-tenrecs (*Microgale* spp.) from eastern and central Madagascar. Journal of Zoology, **235**: 339–350.

SWINDLER, D. R. 1976. Dentition of Living Primates. Academic Press, London, UK, 308 pp.

THOMAS, [M. R.] OLDFIELD. 1882. Description of a new genus and two new species of Insectivora from Mad-

agascar. Journal of the Linnean Society (Zoology), **16:** 319–322.

———. 1884. Description of a new species of *Microgale*. Annals and Magazine of Natural History, series 5, **14:** 337–338.

———. 1918. On the arrangement of the small Tenrecidae hitherto referred to *Oryzorictes* and *Microgale*. Annals and Magazine of Natural History, series 9, **1:** 302–307.

———. 1926. On some small mammals from Madagascar. Annals and Magazine of Natural History, series 9, **17:** 250–252.

Appendix 10-1.

Key to the Genera of Tenrecidae Occurring at RS d'Anjanahribe-Sud.

1. Pelage spinous; tail very short 2

   Pelage soft, lacking spines; tail medium to long 4

2. Closely set, sharp spines cover dorsal surface . . . . *Setifer*

   Dorsal surface covered with a mixture of spines and long, coarse hair 3

3. Dorsal pelage dark with longitudinal pale stripes; head and body length <200 mm . . . . *Hemicentetes*

   Dorsal pelage uniform brown; head and body length >260 mm . . . . *Tenrec*

4. Body robust, forelimbs robust, forefeet broad with enlarged, stout claws; upper canine longer than first upper incisor . . . . *Oryzorictes*

   Body slender to moderately robust, forelimbs not enlarged, forefeet slender to moderately broad, claws short to moderately lengthened; first upper incisor longer or subequal in length to upper canine . . . . *Microgale*

Appendix 10-2.

Key to the Species of *Microgale* Occurring at RS d'Anjanaharibe-Sud.

1. Size very small, HB < 62 mm, CIL < 16.9 mm . . . .*M. parvula*

   Size larger, HB > 65 mm, CIL > 19.0 mm 2

2. Ratio of TL:HB > 2.0 3

   Ratio of TL:HB < 1.5 4

3. Size smaller, HB < 75 mm, CIL < 21.6 mm . . . . *M. longicaudata*

   Size larger, HB > 78 mm, CIL > 22.5 mm . . . .*M. principula*

4. Digits and tail tip contrastingly paler than body, tail, and feet . . . .*M. fotsifotsy*

   Tail tip and digits not obviously paler than rest of body 5

5. Proboscis long, large rhinarium extends posterodorsally onto muzzle; forefeet broad, foreclaws enlarged . . . . *M. gymnorhyncha*

   Small rhinarium confined to anterior of short proboscis; forefeet slender without lengthened foreclaws 6

6. Tail markedly bicolored; ratio of TL:HB < 0.9 . . . . *M. cowani*

   Tail not markedly bicolored; ratio of TL:HB > 0.9 7

7. Body size smaller, HB < 75 mm . .*M. taiva*

   Body size larger, HB > 75 mm 8

8. Cranial size smaller, CIL < 26.5 mm; body size averaging smaller, HB <104 mm 9

   Cranial size larger, CIL > 28.5 mm; body size averaging larger, HB > 99 mm 10

9. Pelage dark brown dorsally, slightly lighter ventrally; TL longer than HB, ratio > 1.2 . . . .*M. monticola*

   Pelage lightish buff brown dorsally, reddish buff ventrally; TL subequal to HB, ratio < 1.1 . . . .*M. soricoides*

10. Cranial size smaller, CIL < 32.0; body size averaging smaller, HB < 112 mm, WT < 31 g . . . .*M. dobsoni*

    Cranial size larger, CIL > 34.5; body size averaging larger, HB > 106 mm, WT > 31 g . . . .*M. talazaci*

Chapter 11

New Taxa of Nesomyine Rodents (Muroidea: Muridae) from Madagascar's Northern Highlands, with Taxonomic Comments on Previously Described Forms

Michael D. Carleton[1] and Steven M. Goodman[2]

Abstract

Field survey of the Réserve Spéciale d'Anjanaharibe-Sud has disclosed previously unknown taxa of Nesomyinae from Madagascar's northern highlands, a vast region heretofore poorly documented for the island's indigenous rodents. We diagnose and compare: a new species of *Eliurus* whose morphology suggests relationship to another recently described form, *E. petteri* from east-central Madagascar; and a new genus and species of Nesomyinae with attributes that indicate closest affinity, among the eight genera currently recognized, to *Eliurus*. The new forms originate from middle montane to sclerophyllous montane forest within the reserve (1250–1950 m). Evidence for the specific status of *E. ellermani* is reviewed, and its type locality is amended. Although museum and field studies in the last decade have revised upwardly the number of Nesomyinae, doubling the number of species known, the expectation that their diversity will match that of rodents on comparably sized tropical islands seems doubtful.

Résumé

L'inventaire mené dans la Réserve Spéciale d'Anjanaharibe-Sud a permis la découverte, au niveau des zones d'altitude du nord de Madagascar, de taxons de Nesomyinae jusqu'alors inconnus, provenant d'une vaste région pourtant fort mal connue sur le plan de la faune endémique des rongeurs. Nous avons établi une diagnose et comparé une nouvelle espèce d'*Eliurus* dont la morphologie laisse à penser qu'elle puisse avoir des relations avec *E. petteri*, une autre espèce récemment décrite du centre-est de Madagascar, et une nouvelle espèce appartenant à un nouveau genre de Nesomyinae dont certains attributs indiquent une proche affinité avec le genre *Eliurus*, un des huit genres actuellement reconnus dans la sous-famille des Nesomyinae. Cette nouvelle forme a été recontrée au sein de la réserve, depuis la forêt de moyenne altitude jusqu'au fourré sclérophylle de montagne, soit entre 1250 et 1950 m d'altitude. L'évidence du statut particulier d'*E. ellermani* est commentée et la localité du type est complétée. Bien que des études muséologiques et de terrain aient, au cours des dix dernières années, permis d'amender considérablement le nombre d'espèces de Nesomyinae, en doublant leur nombre, l'idée que la diversité de ces espèces atteigne la diversité de rongeurs constatée dans des îles tropicales de taille similaire, semble improbable.

[1] Division of Mammals, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560 U.S.A.
[2] Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, IL 60605-2496 U.S.A.

Introduction

To date, few species of Madagascar's indigenous rodents (Muridae: Nesomyinae) have been documented from the rugged northern highlands of the island. For example, the rodent denizens of montane forest and alpine habitat on the vast Tsaratanana Massif, isolated from the Central High Plateau, are virtually unknown: only two species and three specimens of Nesomyinae, one *Eliurus minor* and two *Nesomys rufus*, have been reported previously (Carleton & Schmidt, 1990; Carleton, 1994). The 1994 small mammal survey of the Réserve Spéciale (RS) d'Anjanaharibe-Sud, which straddles the eastern portion of these northern mountains, thus constitutes the first concerted attempt to address this conspicuous geographic void in understanding nesomyine diversity and distribution.

This chapter provides the systematic context and nomenclatural background for certain nesomyine forms reported in Chapter 12, which covers their populations and natural history. Our short prodromus includes the discovery of a new species of *Eliurus*, commentary on the taxonomic status of a previously named form of *Eliurus*, and diagnosis of a new genus and species of Nesomyinae.

Materials and Methods

The material from the RS d'Anjanaharibe-Sud consists of conventional round skins with skulls, as well as complete skeletons and fluid-preserved whole carcasses, and is housed in the Field Museum of Natural History (FMNH), Chicago, and the Département de Biologie Animale, Université d'Antananarivo (UA), Antananarivo. Specimens already deposited in the latter institution are referenced by the collector's field numbers (UA-SMG) in lieu of catalog numbers. Relevant series of Nesomyinae used in the various tabular summaries, numerical analyses, and anatomical comparisons were examined by M.D.C. from the following collections: the American Museum of Natural History (AMNH), New York City; the Natural History Museum (BMNH), London; the Museum of Comparative Zoology (MCZ), Harvard University, Cambridge; the Muséum National d'Histoire Naturelle (MNHN), Paris; and the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C. Museum numbers and locality data are provided in Appendix 11-1.

Six measurements, in millimeters (mm) or grams (g), were taken by S.M.G. for each FMNH specimen in the flesh; their abbreviations and definitions are given below. Dimensions from other museum specimens are those given by collectors on skin tags or in field catalogs. Dry hindfoot length was recorded by M.D.C. to the nearest 0.5 mm, especially on older museum specimens, which typically lack any external data. External measurements are tabulated for the purposes of general description and field identification but were not used in multivariate comparisons of samples.

TOTL = total length of body and tail, measured from the tip of the nose to the end of the caudal vertebrae (not including terminal hair tuft).

HB = head and body length, as measured in the field, from the tip of the nose to the distalmost point of the body (at base of tail).

TL = tail length, measured from the base of the tail (held at right angle to the body) to the end of the last caudal vertebra (not including terminal hair tuft).

HF = hindfoot length, measured from the heel to the tip of the longest toe (not including claw).

DHF = dry hindfoot length, measured from the heel to the tip of the claw of the longest toe, on skins whose metatarsal and phalangeal bones remained straightly aligned.

EL = ear length, measured from the basal notch to the distalmost rim of the pinna.

WT = weight, measured in grams with Pesola spring scales to within 0.5 g for animals weighing less than 100 g and to within 1.0 g for those weighing between 101 and 300 g.

Sixteen cranial and two dental dimensions were measured by M.D.C. to the nearest 0.1 mm using handheld digital calipers accurate to 0.03 mm. These measurements, and their abbreviations, follow the anatomical landmarks defined and illustrated in Carleton (1994):

BBC = breadth of the braincase
BIF = breadth of incisive foramina
BM1s = breadth of the bony palate across the first upper molars

BOC = breadth across the occipital condyles
BR = breadth of rostrum
BZP = breadth of the zygomatic plate
DAB = depth of the auditory bulla
IOB = interorbital breadth
LBP = length of bony palate
LD = length of diastema
LIF = length of the incisive foramina
LM1-3 = coronal length of maxillary tooth row
LR = length of rostrum
ONL = occipitonasal length
PPB = posterior breadth of the bony palate
PPL = postpalatal length
WM1 = width of the first upper molar
ZB = zygomatic breadth

Standard descriptive statistics and multivariate analyses were carried out using Systat (version 7.0, 1996). Morphological terms generally follow Carleton (1980) and Voss (1988); names of dental structures follow Reig (1977), as illustrated by Carleton and Musser (1989); the rationale for various character polarities discussed in the text is elaborated by Hershkovitz (1962), Bugge (1970), Carleton (1980, 1994), Voss (1988, 1993), and Carleton and Musser (1989). Field methods for the FMNH specimens originating from the RS d'Anjanaharibe-Sud are described by Goodman and Carleton in Chapter 12.

The Tufted-Tail Rats, Genus *Eliurus*

Among the rodent collections obtained from moist forest in the RS d'Anjanaharibe-Sud are samples of five species of *Eliurus*. Three of these, *E. majori* Thomas (1895), *E. minor* (Major, 1896a), and *E. webbi* Ellerman (1949), can be confidently associated with forms already described and known from other regions of Madagascar (see Chapter 12 for registration numbers and full provenience). The three can be easily distinguished from one another on the basis of external and cranial size (Figs. 11-1–11-3, Table 11-1) in addition to other qualitative traits of the pelage and skull that define their morphologies (Carleton, 1994). The identity of two species, both with tails tipped with fine white hairs, is problematic and warrants additional commentary and comparisons to justify their specific assignment. One of these forms is described as new to the island's indigenous rodent fauna; the other raises questions about the validity of *E. ellermani* Carle-

ton (1994), a recently named species related to *E. tanala.*

The Smaller White-tailed Species

This medium-sized *Eliurus* was relatively abundant at 1260 m, where 26 individuals were live-trapped within a period of 6 days. Only one was collected at 1550 m, but none was taken at the lowest (875 m) or highest (1950 m) sites surveyed. Specimens of the medium-sized, white-tailed *Eliurus* exhibit several features that recall *E. petteri*, a species named from humid forest in east-central Madagascar (Carleton, 1994), yet it is otherwise strongly differentiated from the latter as well, as detailed below. We name it as a new species.

Eliurus grandidieri, new species
(Figs. 11-1–11-6, 11-11; Table 11-2)

HOLOTYPE—Field Museum of Natural History number 154048, skin and skull of young adult female (original number SMG 7066), collected 20 November 1994 by Steven M. Goodman.

Standard measurements (in mm) from the skin tag of the type include the following: TOTL, 324; HB, 132; TL, 186; HF (without claw), 27 (DHF, as measured by M.D.C. with claw, 28); EL, 21; and WT (in g), 59.5. The female carried two embryos (crown–rump length, 10 mm), one each in the left and right uterine horns. The habitat is noted on the specimen tag as "In upper montane forest. Trap on ground at opening of large hole under root clump and covered with debris."

The condition of the skin is good, although its right side is somewhat tucked due to uneven drying of the specimen (Fig. 11-4). The condition of the skull is excellent, its cranial and mandibular processes wholly intact (Fig. 11-5).

TYPE LOCALITY—Madagascar, Province d'Antsiranana, Réserve Spéciale d'Anjanaharibe-Sud, 11 km WSW of Befingitra, 1550 m, 14°44.5'S, 49°27.5'E (as given by the collector).

DIAGNOSIS—A species of *Eliurus* characterized by medium size (HB ≃ 125–135 mm, HF ≃ 27–29 mm, ONL ≃ 34–35.5 mm), in general larger than *E. minor* and smaller than *E. petteri* or *E. webbi*. Dorsal pelage finely textured and dark, underparts dark gray (bright white in *E. petteri*); tail having weakly developed terminal tuft of white hairs (dark to tip in *E. petteri*), caudal vertebrae
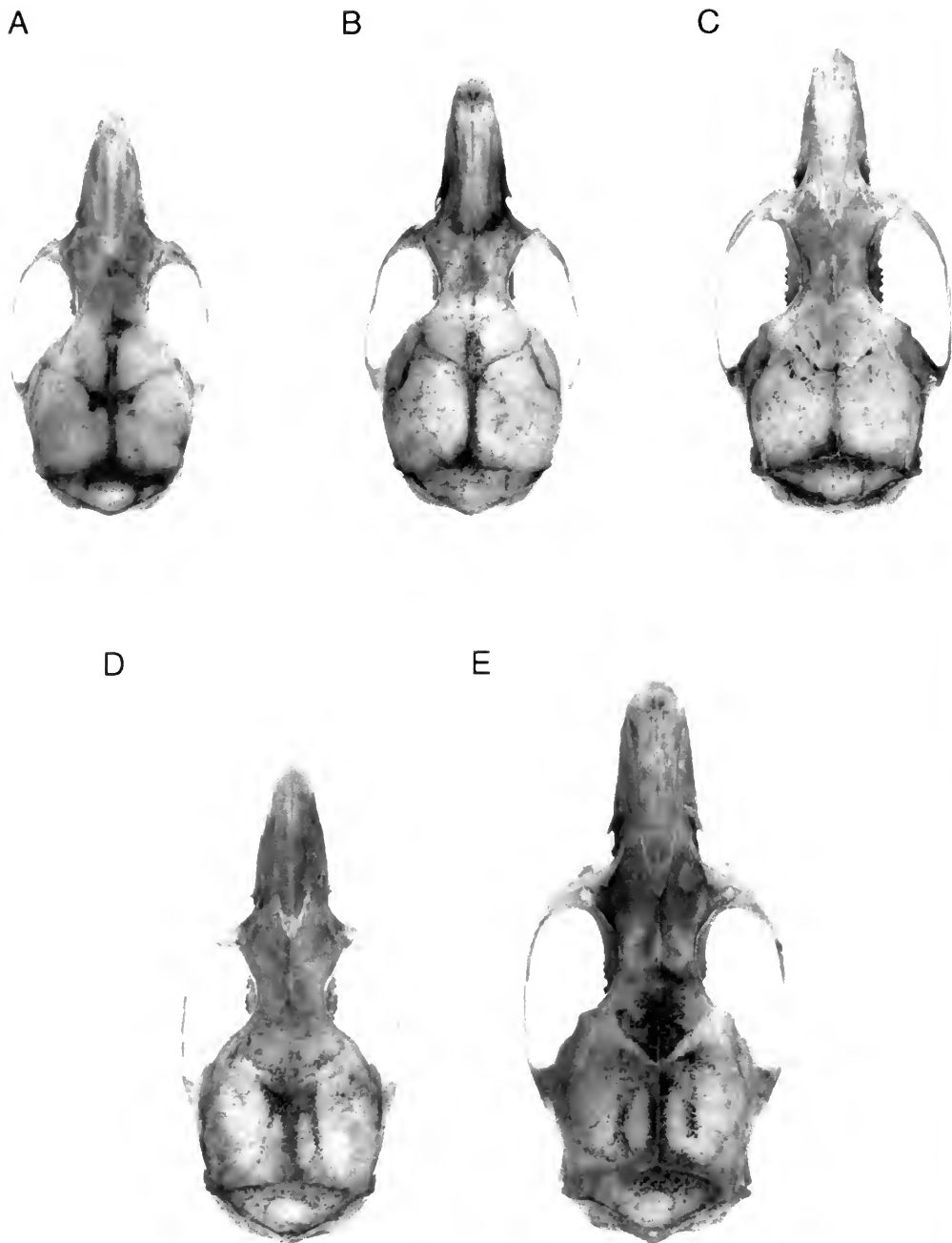
FIG. 11-1. Dorsal view (×1.75) of adult crania of the five species of *Eliurus* that occur in the RS d'Anjanaharibe-Sud. **A,** *E. minor* (FMNH 154042: male, ONL = 32.0 mm). **B,** *E. grandidieri*, new species (FMNH 154048: female, holotype, ONL = 35.3 mm). **C,** *E. majori.* (FMNH 154054: female, ONL = 37.8 mm). **D,** *E. webbi* (FMNH 154251: male, ONL = 38.2 mm). **E,** *E. tanala* (FMNH 154250: female, ONL = 45.7 mm).

relatively long (TL 127% of HB) for the genus (TL 115–120% of HB in most species); and narrow dusky streak extending over middle of metatarsus. Cranium possessing moderately expansive zygomatic arches (bowed little in *E. petteri*), tiny ectotympanic bullae, and moderately long and wide incisive foramina (very short and narrow in *E. petteri*); mandible lacking capsular process, in-
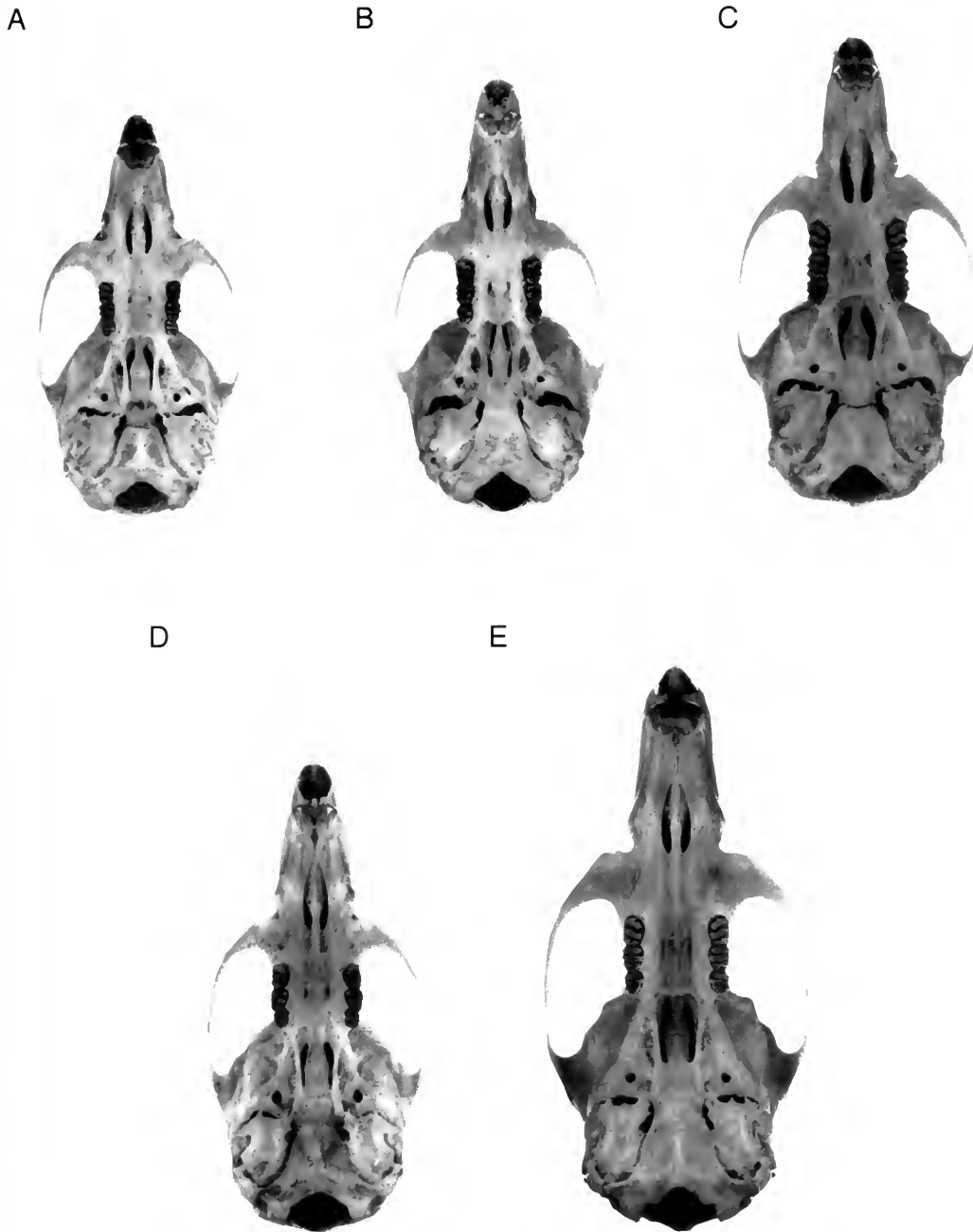
FIG. 11-2. Ventral view (×1.75) of adult crania of the five species of *Eliurus* that occur in the RS d'Anjanaharibe-Sud. **A**, *E. minor*. **B**, *E. grandidieri*, new species. **C**, *E. majori*. **D**, *E. webbi*. **E**, *E. tanala*. Same specimens as illustrated in Figure 11-1.

cisor alveolus extremely short; upper and lower incisors among the narrowest in the genus (only matched by *E. petteri*), but molar rows somewhat long and robust.

REFERRED SPECIMENS—Province d'Antsiranana,

RS d'Anjanaharibe-Sud, 9.2 km WSW of Befingi-tra, 1260 m, 14°44.7′S, 49°27.7′E (FMNH 154046, 154047, 154253–154257, 154259–154265, 154288, 154290–154292; UA-SMG 6913, 6936, 6937, 6944–6946, 7002, 7006). All referred specimens were also
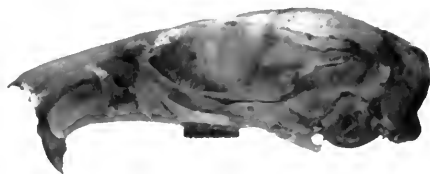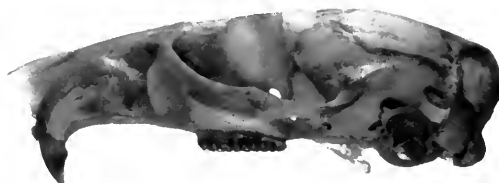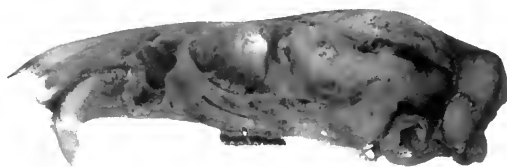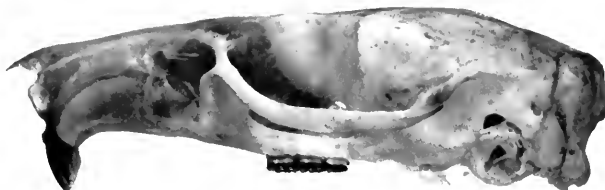
FIG. 11-3. Lateral view (×1.75) of adult crania of the five species of *Eliurus* that occur in the RS d'Anjanaharibe-Sud. **A**, *E. minor.* **B**, *E. grandidieri*, new species. **C**, *E. majori.* **D**, *E. webbi.* **E**, *E. tanala.* Same specimens as illustrated in Figures 11-1 and 11-2.

TABLE 11-1. Comparison of selected external and craniodental measurements of *Eliurus minor*, *E. webbi*, and *E. majori*, the three dark-tailed species from the RS d'Anjanaharibe-Sud.*

Variable	E. minor[†]	E. webbi[‡]	E. majori[§]
TOTL	244.0 ± 16.9	309.7 ± 14.4	354.4 ± 11.4
	205.0–260.0	294.0–332.0	330.0–370.0
HB	110.4 ± 4.4	142.0 ± 4.8	158.6 ± 3.4
	105.0–116.0	138.0–149.0	155.0–165.0
TL	127.7 ± 14.6	163.5 ± 10.1	186.6 ± 8.9
	94.0–139.0	153.0–179.0	170.0–202.0
HF	22.1 ± 0.8	27.7 ± 1.5	29.3 ± 1.1
	21.0–23.0	26.0–29.0	27.0–31.0
WT	36.9 ± 4.1	71.9 ± 5.9	94.2 ± 10.5
	31.0–43.5	63.5–78.5	78.0–109.0
ONL	32.0, 32.3	38.2 ± 0.7	38.4 ± 1.0
		37.2–39.1	36.5–39.8
ZB	15.8, 15.9	17.9 ± 0.6	19.1 ± 0.7
		17.1–18.8	18.3–20.6
BBC	12.2, 12.3	14.0 ± 0.3	14.2 ± 0.3
		13.6–14.3	13.8–14.8
IOB	5.1, 5.4	5.7 ± 0.2	5.3 ± 0.1
		5.3–5.9	5.2–5.5
LR	10.6, 10.9	13.4 ± 0.5	13.3 ± 0.7
		12.5–14.0	12.1–14.3
BR	5.5, 6.0	7.0 ± 0.5	7.1 ± 0.3
		6.6–7.9	6.6–7.6
PPL	11.2, 11.3	13.6 ± 0.7	13.6 ± 0.5
		13.0–14.9	12.7–14.4
LBP	6.6, 6.9	8.0 ± 0.4	7.6 ± 0.4
		7.3–8.3	7.1–8.1
LIF	4.0, 4.6	5.5 ± 0.2	6.2 ± 0.4
		5.3–5.8	5.7–6.9
BIF	2.0, 2.1	2.1 ± 0.1	2.6 ± 0.1
		2.0–2.4	2.4–2.9
LD	9.1, 9.3	11.1 ± 0.3	10.9 ± 0.5
		10.8–11.6	10.2–11.6
BM1s	5.9, 6.5	7.4 ± 0.2	7.9 ± 0.2
		7.1–7.6	7.5–8.3
DAB	4.7, 4.9	5.1 ± 0.1	5.3 ± 0.3
		5.0–5.2	5.2–6.0
BZP	2.6, 2.9	3.2 ± 0.1	3.3 ± 0.2
		3.0–3.4	3.0–3.6
BOC	6.8, 7.3	8.3 ± 0.2	8.5 ± 0.4
		7.9–8.6	7.9–8.9
LM1-3	4.29, 4.39	5.10 ± 0.15	6.62 ± 0.12
		4.90–5.31	6.40–6.78
WM1	1.20, 1.25	1.44 ± 0.07	1.73 ± 0.08
		1.34–1.54	1.60–1.81

* Sample statistics include the mean ± 1 SD and the observed range.

† For external variables, N = 8 (FMNH 154042, 154043, and 154246–154248; UA-SMG 6880, 6974, and 6980); for cranial variables, N = 2 (FMNH 154042 and 154043).

‡ For external and cranial variables, N = 6 (FMNH 154035–154038, 154251, and 154252).

§ For external variables, N = 11 (FMNH 154052–154054, 154242–154245, and 154289; UA-SMG 6981, 6998, and 7090); for cranial variables, N = 9 (FMNH 154052–154054, 154242–154245, 154266, and 154289).

collected by S.M.G. between 4 and 9 November 1994 as part of the same inventory and variously prepared as skin with skull, complete skeleton, fluid-preserved carcass with skull removed, or whole carcass in fluid.

DISTRIBUTION—At present known only from moist montane forest between 1260 and 1550 m in the RS d'Anjanaharibe-Sud. The species may be expected in other highlands of northern Madagascar, e.g., the Tsaratanana massif.

MORPHOLOGICAL DESCRIPTION—Caudal pilosity weakly expressed (tuft much less developed com-
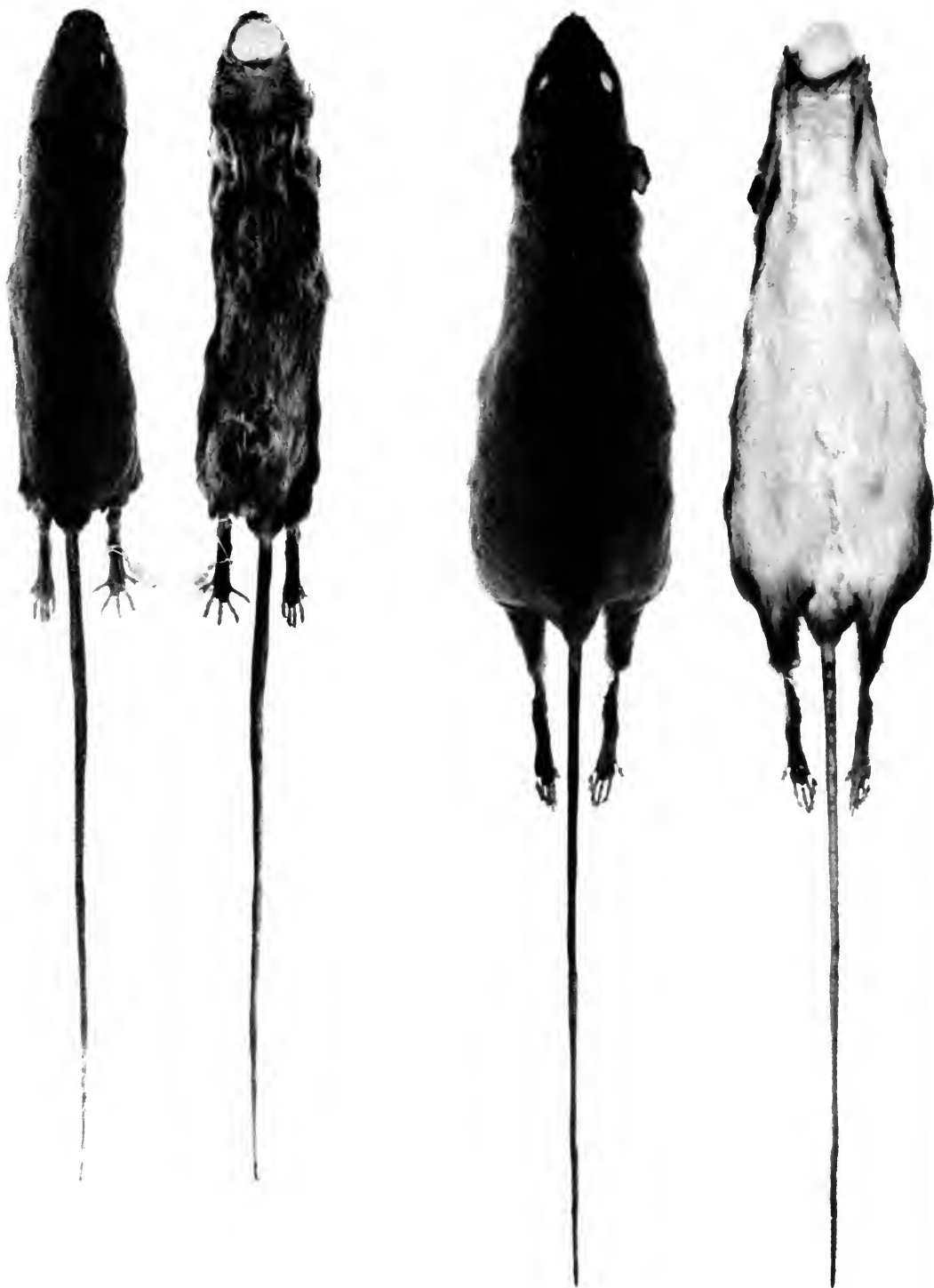
FIG. 11-4. Dorsal and ventral aspects of the skins of *Eliurus grandidieri*, new species (FMNH 154048: holotype; Antsiranana Province, RS d'Anjanaharibe-Sud) (**left pair**), and *E. petteri* (USNM 341825: paratype; Toamasina Province, 18 km E of Périnet) (**right pair**).

FIG. 11-5. Dorsal, ventral, and lateral views of the cranium and lateral view of the mandible of the holotype (FMNH 154048: ONL = 35.3 mm) of *Eliurus grandidieri*, new species.

pared with the smaller *Eliurus minor*), with noticeable penicillate section limited to distal 25–30% of tail length and the hairs short, 7–8 mm. Tail tipped with fine white hairs, this terminal white tuft varying from 15 to 35 mm long (Fig. 11-11). Caudal epidermis unpigmented over terminal segment, coincident with extent of white tuft; proximal 70–75% of tail length pigmented dark gray dorsally, irregularly mottled with white splotches ventrally (i.e., not sharply or evenly bicolored). Proximal scutellation moderately coarse, about like *E. minor* but heavier than *E. petteri*; basal scale hairs short (about one annulation long) and inconspicuous, tail appearing naked over proximal half.

Dorsal pelage relatively short and close set (8–9 mm on midrump), texture fine and soft, conveying a sleek appearance. Cover hairs of dorsum tricolored, long basal segment of plumbeous gray, short middle band of warm buff, and very short tip of dark brown to blackish; guard hairs dark brown but inconspicuous, extending only slightly above cover fur. General effect of upperparts a sooty brown to charcoal gray, denser concentration of black toward mediodorsum and browner on flanks, overall tone somber. Narrow dusky streak over tarsus and metatarsus usually well defined; remainder of metatarsus and phalanges, including ungual tufts over claws, clothed with clear white hairs; tops of forefeet white, dark dorsal pelage ending at carpus. Ventral cover hairs bicolored, basal two-thirds plumbeous gray, and distal third dull to clear white; general impression of underparts a medium to dark gray, distinct from but not sharply contrasted with muted dorsum. Longest mystacial vibrissae about 40–50 mm, extending behind pinnae when appressed to skin; genal vibrissae extremely short (absent?). Pinnae dark, appearing naked to unaided eye, but invested externally with short brown hairs and internally with fine white ones.

Skull moderate in size and construction, intermediate to *Eliurus minor* and *E. webbi* in general aspect but with a proportionally longer rostrum (Figs. 11-1–11-3; Tables 11-1, 11-2). Configuration of interorbital region, braincase, and zygomatic plate as per the genus (Carleton, 1994). Zygomatic arches moderately stout for size of skull, deeper over midsection than delicate arches of *E. petteri*; lateral bowing more pronounced toward rear of zygoma, at squamosal–jugal contact, and converging toward zygomatic plates. Incisive foramina typical for the genus, about 46% of diastemal length, longer and wider than those of *E. petteri* (LIF about 38% of LD). Posterior palatal foramina formed as a single pair of small oval openings, no development of supernumerary palatal perforations or elongate slits as in some *Eliurus* (such as *E. minor* and *E. tanala*). Anterior margin of mesopterygoid fossa broadly horseshoe-shaped, extending slightly between third molars, about one-third their length. Subsquamosal fenestra and postglenoid foramen open fully in all specimens, revealing lumen of braincase, hamular process neatly delineated. Alisphenoid strut present on holotype, but of 12 specimens with cleaned skulls, four without any evidence of this bony partition between the buccinator–masticatory and accessory oval forami-

TABLE 11-2. Comparison of selected external and craniodental measurements of *Eliurus grandidieri*, new species, and *E. petteri* Carleton (1994).*

Variable	*E. grandidieri* (Holotype)[†]	*E. petteri* (Holotype)[‡]	*E. grandidieri* (Type Series)[§]	*E. petteri* (Type Series)[‖]
TOTL	324.0		293.4 ± 13.4 275.0–324.0	314.0
HB	132.0	130.0	127.3 ± 4.4 118.0–135.0	133.0 130.0, 136.0
TL	186.0	185.0	161.7 ± 12.3 141.0–186.0	181.5 178.0, 185.0
HF	28.5	33.0	27.7 ± 0.8 26.0–29.0	33.5 33.0, 34.0
WT	59.5		52.8 ± 5.5 44.5–67.5	74.0
ONL	35.3	38.4	34.7 ± 0.6 33.5–35.6	38.3 ± 0.6 37.6–38.8
ZB	17.6	17.9	16.8 ± 0.9 15.0–17.8	17.2 ± 0.7 16.6–17.9
BBC	13.5	13.8	13.1 ± 0.5 12.4–14.0	13.4 ± 0.3 13.1–13.8
IOB	5.5	5.2	5.4 ± 0.1 5.2–5.6	5.4 ± 0.2 5.2–5.6
LR	12.9	13.9	12.4 ± 0.3 11.9–12.9	13.5 ± 0.5 13.0–13.9
BR	6.4	6.7	6.3 ± 0.3 5.9–7.0	6.6 ± 0.1 6.5–6.7
PPL	11.9	13.4	11.7 ± 0.4 10.8–12.2	13.5 ± 0.4 13.1–13.9
LBP	7.7	8.4	7.3 ± 0.3 6.7–7.7	8.1 ± 0.5 7.6–8.4
LIF	4.4	4.1	4.7 ± 0.3 4.3–5.0	4.0 ± 0.2 3.7–4.1
BIF	2.2	2.1	2.2 ± 0.2 2.0–2.7	2.0 ± 0.1 1.9–2.1
LD	10.0	10.9	10.1 ± 0.3 9.3–10.4	10.6 ± 0.3 10.4–10.9
BM1s	6.8	6.9	6.9 ± 0.2 6.5–7.2	6.9 ± 0.3 6.6–7.1
DAB	5.0	5.2	4.5 ± 0.2 4.1–5.0	5.0 ± 0.2 4.8–5.2
BZP	3.0	3.3	3.1 ± 0.2 2.7–3.4	3.2 ± 0.1 3.1–3.3
BOC	7.9	8.3	7.8 ± 0.2 7.3–8.0	8.2 ± 0.1 8.0–8.3
LM1-3	5.38	5.05	5.42 ± 0.11 5.29–5.63	5.01 ± 0.1 4.90–5.09
WM1	1.56	1.38	1.52 ± 0.05 1.43–1.61	1.40 ± 0.06 1.35–1.47

* Sample statistics include the mean ± 1 SD and the observed range.
[†] FMNH 154048.
[‡] MNHN 1961.177
[§] For external variables, N = 19–23 (FMNH 154046–154048, 154253, 154254, 154256, 154257, 154259, 154260, 154262–154264, 154288, 154290, and 154291; UA-SMG 6913, 6936, 6937, 6944–6946, 7002, and 7006); for cranial variables, N = 12 (FMNH 154046–154048, 154257, 154262, 154265, 154288, and 154290–154292; UA-SMG 6936 and 6945).
[‖] For external variables, N = 1 or 2 (MNHN 1961.177; USNM 341825) ; for cranial variables, N = 3 (MCZ 45928; MNHN 1961.177; USNM 341825).

na. Ectotympanic bullae tiny, relatively as small as those of *E. petteri*, wide posteroventral expanse of periotic correspondingly visible.

Upper and lower incisors delicate, thin in width and depth like those of *Eliurus petteri*; enamel face of incisors yellow to very pale orange. Upper incisors more nearly orthodont; alveolus of lower incisor short, terminating at the level of the coronoid process and low on the ascending ramus, without lateral protuberance as a capsular process. Upper and lower third molars shorter than second molars as in most *Eliurus*, unlike relatively large third molars of *E. majori* and *E. penicillatus*.

NOTES ON NATURAL HISTORY—Individuals of *Eliurus grandidieri* occurred sympatrically with those of *E. majori*, *E. minor*, *E. tanala* (see following account), *Gymnuromys roberti*, and *Nesomys rufus*, as well as the ubiquitous commensal *Rattus rattus*. Several of these nesomyines are themselves restricted to middle or upper montane zones (*E. majori*, *E. tanala*, and *N. rufus*) or are widely ranging in altitudinal occurrence (*E. minor* and *G. roberti*).

ETYMOLOGY—The species epithet, *grandidieri*, recognizes the early contributions of the explorer and naturalist Alfred Grandidier to understanding Madagascar's unique biota and insular geography. The elder Grandidier was among the first to appreciate the uniqueness of the fauna, including its rodents. He discovered the first examples of and later described the giant rat *Hypogeomys antimena* (Grandidier, 1869) and collected the first specimen of a tufted-tail rat, later described by Milne Edwards (1885) as the type species, *myoxinus*, of his new genus *Eliurus*.

TAXONOMIC COMPARISONS—Grandidier's tufted-tailed rat is an attractive and distinctive species. At first glance, its external appearance suggests a gracile version of *Eliurus tanala*, and its skull resembles an oversized example of *E. minor* with a longer rostrum. In external and cranial dimensions, *E. grandidieri* surpasses examples of *E. minor* but is notably smaller than those of *E. webbi* and *E. majori* (compare Tables 11-1 and 11-2). Its terminal caudal plume of white hairs offers clear-cut visual separation from examples of the latter three species, all of which have completely dark-furred tails. The robust size of the second species with a white-tipped tail, whose taxonomic assignment is discussed next, permits no confusion with the much smaller *E. grandidieri*. In addition to size and a long tail with a terminal white tuft, the short alveolus of the lower incisor and the absence of a capsular process segregate *E. grandidieri* from other species of *Eliurus* found in the reserve (Figs. 11-6, 11-11). Extended comparison and contrast are required to only one other species, *E. petteri*, a form known by just three specimens from three nearby localities in the vicinity of RS d'Analamazaotra, east-central Madagascar (Carleton, 1994).

Eliurus grandidieri and *E. petteri* share certain anatomical traits that are uncommon among described forms of *Eliurus* and that implicate each as the other's closest relative within the genus. The dorsal pelage of both appears sleek and relatively short, its texture fine and soft; the color is dark and the tone muted. The dark color of the upperparts extends onto the metatarsi of both species as a median dusky streak. The two have a weakly developed terminal caudal tuft, the hairs short and the notably penicillate expansion confined to the distal one-quarter of tail length (distal one-third or more in other *Eliurus*); the contrast is well conveyed by comparison to the dense, long caudal tuft characteristic of the smaller-bodied *E. minor*. In spite of the undistinguished terminal tuft, the tails of *E. grandidieri* and *E. petteri* are relatively the longest in the genus, about 125–135% of head and body length compared with 115–120% in most *Eliurus*. Other proportional similarities include their uninflated ectotympanic bullae, which are relatively the smallest within the genus (the absolute depth of the bulla is approximately equal to that of the smaller *E. minor*; Tables 11-2, 11-7), and the exceptionally delicate construction of their upper and lower incisors, again qualifying as extreme in this regard for the genus. The three known individuals of *E. petteri* and a minority of *E. grandidieri* specimens (four of 12 skulls) lack an alisphenoid strut, a feature whose absence is interpreted as derived; the strut is uniformly present on all specimens of other *Eliurus* species so far examined (Carleton, 1994). Lastly, the lower incisor of both species lacks any lateral protrusion as a capsular process and is unusually short, ending at the level of the coronoid process and low on the ascending ramus (Fig. 11-6). In other *Eliurus*, the alveolus of the lower incisor terminates as a discernable lateral bulge set more dorsad and rearward on the ascending ramus.

Although such singular resemblances of *Eliurus grandidieri* and *E. petteri* offer preliminary support for their close kinship, as many differences highlight their status as separate species.
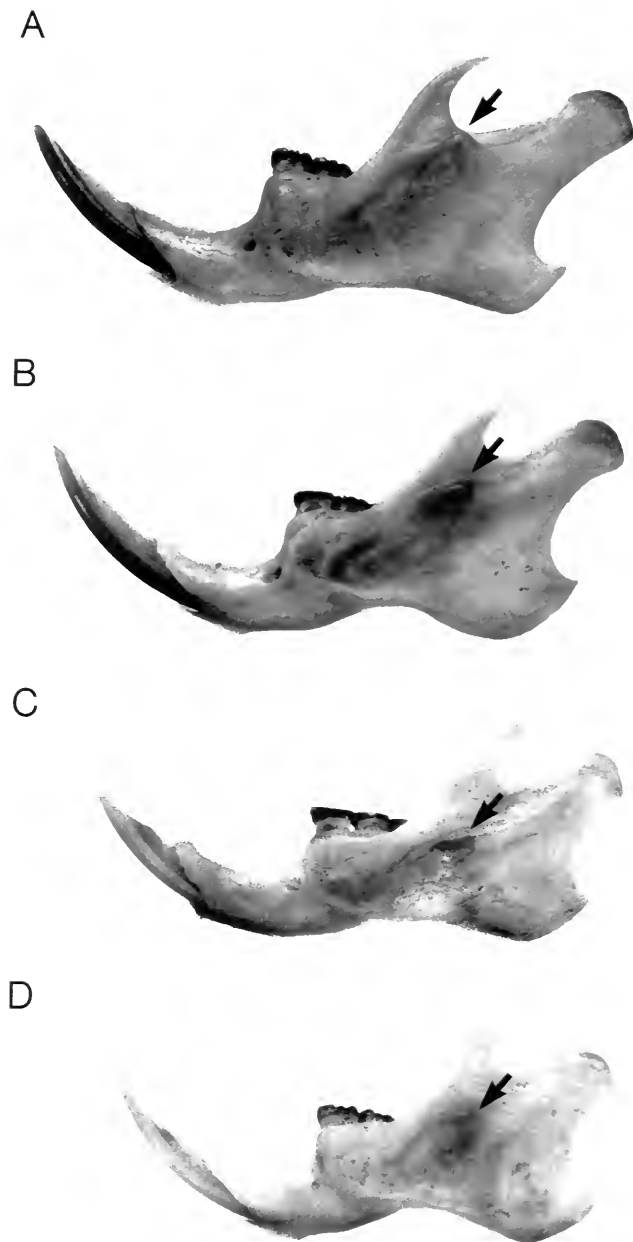
FIG. 11-6. Lateral view (×3) of left mandibles of four species of *Eliurus*. **A,** *E. tanala* (USNM 448983: Ambodiamontana). **B,** *E. webbi* (USNM 448993: 0.5 km N of Kianjavato). **C,** *E. petteri* (USNM 341825: 18 km E of Périnet). **D,** *E. grandidieri*, new species (FMNH 154048: RS d'Anjanaharibe-Sud). Arrows point to the dorsalmost and posteriormost extension of the incisor alveolus.

Two chromatic traits of the skin provide externally obvious means of discrimination: the definition of the tail tuft, white-tipped in *E. grandidieri* versus brownish gray in *E. petteri* (Fig. 11-11), and the dorsal–ventral pelage contrast, gray venter in *E. grandidieri* versus bright white underparts in *E. petteri* (Fig. 11-4). *E. petteri* is the bigger of the two species, as judged by most measurements of the skin and skull (Table 11-2). Although larger in most extremal dimensions, the thin zygoma and longer, narrow rostrum of *E. petteri* convey a more gracile cranial construc-
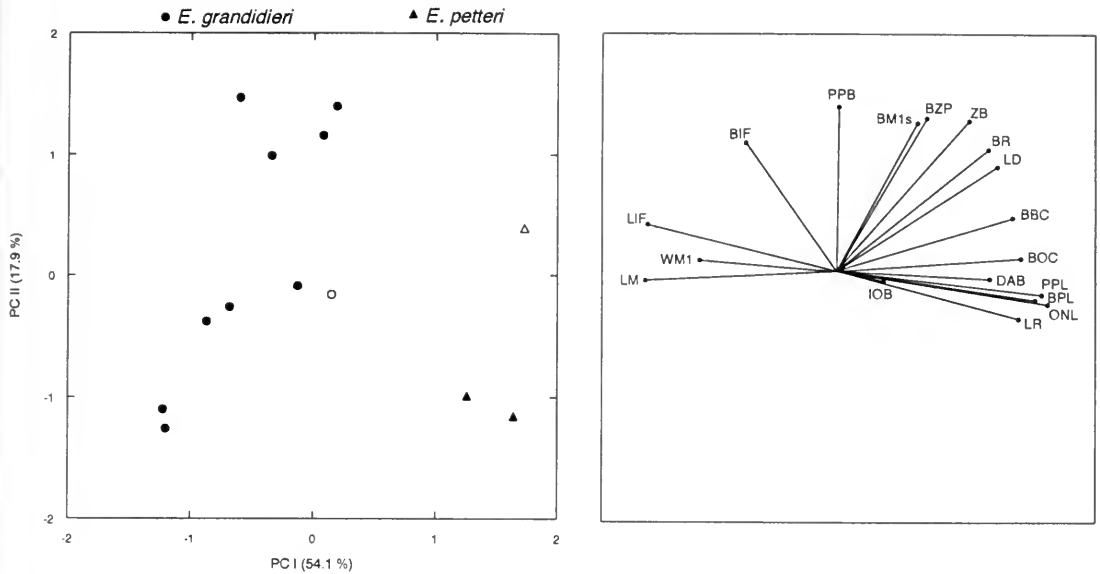
FIG. 11-7. Results of principal components analysis of 18 log-transformed craniodental variables measured on intact specimens of *Eliurus grandidieri* (N = 10) and *E. petteri* (N = 3). **Left,** Projection of individual scores onto the first two principal components (open symbols represent the type specimens). **Right,** Vectors of the 18 craniodental variables corresponding to the magnitude and direction of their loadings on the first and second principal components (also see Table 11-3).

tion in contrast to the wider zygomatic arches and shorter, broad rostrum typifying the skull of *E. grandidieri*. Furthermore, the absolutely and relatively larger incisive foramina and molars of the latter species enhance its robust appearance.

Such size and shape dissimilarities are reflected in ordination analyses of log-transformed measurements of all intact crania representing the two species. Most dimensions display large, positive correlations with the first principal component extracted and contribute to the hiatus between *Eliurus grandidieri* and *E. petteri* along that axis (Fig. 11-7, Table 11-3). Exceptions to this pattern include measurements of the molars (LM1-3 and WM1) and incisive foramina (LIF and BIF), which load negatively at moderate to strong levels on the first principal component (Table 11-3). The appreciable variation summarized by the second principal component, especially the spread among specimens of *E. grandidieri*, is plausibly attributed to age-related size increase in certain variables. This influence is particularly notable for many cranial breadths of the facial skeleton (such as BIF, BM1s, BR, BZP, and ZB), but less so for those dimensions measured across the braincase (BBC, BOC, and IOB). Age class, as an independent factor, significantly affects ($F = 7.2$, $P = 0.02$, and df = 7) the dispersion of PC II scores

among specimens of *E. grandidieri* (not calculable for the small sample of *E. petteri*).

The Larger White-tailed Species

Among the five species of *Eliurus* collected within the RS d'Anjanaharibe-Sud, the second species with a white caudal tuft is unmistakable by virtue of size alone, e.g., the big hindfoot (HF > 32 mm) and generously proportioned skull (ONL > 42 mm). Seven examples (only four adults with skulls) of this distinctive form were obtained from the transect stations at 875 and 1260 m. A white caudal tuft characterizes samples of *E. tanala*, another large species so far known from midelevation humid forest (455–1625 m) that stretches from the Réserve Naturelle Intégrale (RNI) d'Andringitra to the vicinity of Lac Alaotra (Carleton, 1994; Goodman & Carleton, 1996). On the other hand, such robust dimensions equally recall those of *E. ellermani*, a dark-tailed form recently described by Carleton (1994) on the basis of two specimens from northeastern Madagascar (type locality = Hiaraka, see below).

The pelage and cranial attributes observed in the series from the RS d'Anjanaharibe-Sub raise doubts about the conservativism of certain features ad-

TABLE 11-3. Results of principal component analysis and one-way ANOVA performed on 18 log-transformed craniodental dimensions of specimens of *Eliurus grandidieri* (N = 10) and *E. petteri* (N = 3) (see also Fig. 11-7).

| Variable | Correlations | | *F* (species) |
	PC I	PC II	
ONL	0.96	−0.15	76.1***
ZB	0.61	0.70	0.7
BBC	0.80	0.25	4.8
IOB	0.21	−0.05	0.0
LR	0.83	−0.22	18.7**
BR	0.69	0.57	2.0
PPL	0.94	−0.11	37.6***
LBP	0.91	−0.13	20.9**
LIF	−0.87	0.22	16.4**
BIF	−0.42	0.60	8.0*
LD	0.76	0.49	4.9*
BM1s	0.37	0.69	0.0
PPB	0.01	0.77	0.1
DAB	0.70	−0.03	9.0*
BZP	0.41	0.71	0.3
BOC	0.84	0.06	10.9**
LM1-3	−0.88	−0.04	32.7***
WM1	−0.63	0.05	12.4**
Eigenvalue	0.027	0.009	
% Variance	54.1	17.9	

$^* P \leq 0.05$; $^{**} P \leq 0.01$; $^{***} P \leq 0.001$.

vanced as diagnostic of *Eliurus ellermani* and its status as a species distinct from *E. tanala*. We explore these questions in this section in order to provide a firm identification of the larger white-tailed species. In addition to the two known individuals of *E. ellermani*, the following five series (OTUs) of *E. tanala* were consulted to broaden the comparative scope and estimate of infraspecific variation (see Appendix 11-1 for catalog numbers and specific locality data): RS d'Analamazaotra (N = 17), Parc National (PN) de Ranomafana (N = 18), Vinanitelo (N = 3, including the holotype), RNI d'Andringitra (N = 14), and RNI d'Andohahela (N = 16).

MORPHOLOGICAL AND MORPHOMETRIC COMPARISONS—Carleton (1994: p. 39) framed the diagnosis of *Eliurus ellermani* on the combination of the form's robust size and dark caudal tuft.

"A large (ONL = 42–44 mm, DHF = 33–34 mm) species of *Eliurus* that resembles a robust version of *E. tanala* except with the tail brush completely dark to the tip; skull stoutly constructed, especially as seen in its broader interorbit, braincase, and expanse of zygomatic arches."

Based on their uniform possession of a white tail tuft (ranging from 12 to 45 mm long on three skins), the RS Anjanaharibe-Sud series agrees with individuals of *Eliurus tanala* and fails to meet an important criterion in the definition of *E. ellermani*. However, their resemblance to *E. ellermani* in other traits is remarkably fine. With regard to size, linear dimensions of the four adults circumscribe those of the two *E. ellermani* specimens (Table 11-4) and average larger than typical *E. tanala* in most aspects (Table 11-6). Still, they can be matched by individuals of the latter species from other localities, particularly those from around the RS d'Analamazaotra (Périnet and Lohariandava). Also, the underparts of the RS Anjanaharibe-Sud animals are monocolored, a dingy creamy white to creamy buff from chin to inguinum (unlike the bright white venter of *E. petteri*), and contrast sharply with the dark grayish brown of the dorsum. This color pattern conforms to the holotype of *E. ellermani* (MNHN 1981.871), but ventral hairs of the paratype (BM(NH) 47.1623) exhibit some basal gray banding to give a slightly darker cast. In addition to bigness and fur color, the seven RS Anjanaharibe-Sub specimens share a number of qualitative traits with *E. ellermani*, namely, the coarsely defined caudal scutellation, fenestrated bony palate, nearly occluded subsquamosal fenestra and correspondingly broad hamular process, and a pronounced capsular process terminating high on the mandibular ramus. Examples of *E. tanala* also display the same character suite (Carleton, 1994).

TABLE 11-4. Comparison of selected external and craniodental measurements of the holotype (MNHN 1981.871) and paratype (BMNH 47.1623) of *Eliurus ellermani* with the larger white-tailed *Eliurus* from the RS d'Anjanaharibe-Sud, here assigned to *E. tanala* (N = 4–5).*

Variable	E. ellermani Holotype	E. ellermani Paratype	E. tanala Anjanaharibe-Sud
TOTL			361.5 ± 16.1
			342.0–381.0
HB	152.0		167.8 ± 4.3
			163.0–174.0
TL	177.0		187.2 ± 17.3
			158.0–203.0
HF	35.0		33.3 ± 0.5
			33.0–34.0
DHF	34.0	33.0	34.0, 35.0
WT			105.9 ± 12.0
			96.5–120.0
ONL	43.8		44.1 ± 1.2
			43.0–45.7
ZB	18.8	20.6	21.1 ± 0.5
			20.3–21.5
BBC	15.2	15.7	15.4 ± 0.3
			14.9–15.7
IOB	6.3	6.3	5.9 ± 0.2
			5.5–6.0
LR	15.1	16.1	15.9 ± 0.8
			14.8–16.6
BR	8.1	8.3	7.6 ± 0.4
			7.2–8.0
PPL	15.5		15.2 ± 0.3
			14.7–15.5
LBP	9.2	10.7	10.5 ± 0.7
			9.7–11.4
LIF	5.8	5.4	5.7 ± 0.3
			5.3–6.0
BIF	2.3	2.2	2.1 ± 0.1
			2.0–2.3
LD	13.4	13.4	13.9 ± 0.6
			13.1–14.5
BM1s	8.4	7.9	8.3 ± 0.3
			8.0–8.6
DAB	5.1	5.3	5.3 ± 0.2
			4.9–5.5
BZP	4.0	4.1	4.2 ± 0.1
			4.1–4.3
BOC	9.3		9.2 ± 0.4
			8.7–9.8
LM1-3	5.82	5.58	5.92 ± 0.25
			5.51–6.22
WM1	1.61	1.63	1.65 ± 0.07
			1.58–1.75

* Sample statistics include the mean ± 1 SD and the observed range.

Nor do covariation patterns revealed in ordinations of craniodental data supply clear-cut evidence for specific separation of the RS Anjanaharibe-Sud animals from the holotype of *Eliurus ellermani* or from examples of *E. tanala*. The first two principal components extracted summarized 41.8 and 11.6% of sample variation, respectively, but divulged no taxonomically meaningful discrimination among the population samples (results not figured); indeed, age class (three classes) as a post hoc explanatory effect influenced the dispersion of individual scores along the first component as strongly ($F = 9.3$, $P \leq 0.001$, and df = 58), as did membership in the six OTUs ($F = 4.2$,

$P \le 0.01$, and df = 55). In like manner, discriminant function analysis of the six population samples produced no discrete subdivisions that suggest specific-level differentiation. Plots of the first two canonical variates portray ambiguous scatter of the data points and appreciable overlap among the six OTUs (Fig. 11-8); loadings of the original variables are generally positive but low to moderate in strength (Table 11-5); and F values derived from one-way ANOVAs for OTU effects, although significant for many variables (df = 55), are generally small (Table 11-5). Trenchant contrasts of size and/or shape, at magnitudes indicative of specific divergence among our six OTUs, are not apparent from this collection of results.

What interpretable structure does emerge from discriminant analysis suggests a weak size cline, from smaller in the south (Andohahela) to larger in the north (Anjanaharibe-Sud). Such an interpretation is consistent with the array of group centroids along the first canonical variate (Fig. 11-8), the geographic associations of population samples generated from Mahalanobis distances among their centroids (Fig. 11-9), and differences among the means of individual variables (Tables 11-4 and 11-6). Although clearly the largest in average size among the samples analyzed, the specimens from RS Anjanaharibe-Sud do not appear inherently different from those of *Eliurus tanala* from farther south. Furthermore, based on these analytical results alone, the type specimen of *E. ellermani* (MNHN 1981.871) appears as another example of the larger-bodied populations that inhabit the northern sector of Madagascar. According to posterior probabilities of group membership, the holotype of *E. ellermani* actually clusters ($P = 0.95$) with the series from the RS d'Analamazaotra instead of the geographically closer RS d'Anjanaharibe-Sud (Fig. 11-8).

SUMMARY AND EMENDED DIAGNOSIS—The specimens of large, white-tailed *Eliurus* from the reserve are provisionally assigned to *E. tanala*. An increase in size, apparently clinal, is observed in populations of *E. tanala* from the RNI d'Andohahela (24.6°S) to the vicinity of the RS d'Analamazaotra (18.5°S) and finds it most robust expression, we hypothesize, in these northern highlands, as represented by the individuals from the RS d'Anjanaharibe-Sud. Moreover, invasive patches of cream-colored hairs on the ventrum occur sporadically in the series from the RS d'Analamazaotra and PN de Ranomafana; those from the RNI d'Andringitra and RNI d'Andohahela uniformly retain the medium gray underparts typical of *E. tanala*. Dominance or fixation of this chromatic variant may be expected in isolation, such as populations in the northern highlands separated from the main distribution of *E. tanala* along the eastern flanks of the Central High Plateau. Perhaps it is relevant that certain northern samples of *E. webbi*, whose distribution parallels that of *E. tanala* in eastern forest, although at lower elevations, also exhibit a high proportion of individuals with a creamy venter (Carleton, 1994). Finally, as circumstantial argument, we note that the altitudinal and habitat stratifications between the large, white-tailed species (875 and 1260 m) and *E. webbi* (only at 875 m) in the RS d'Anjanaharibe-Sud conform with the relationship documented for the two species farther south. Populations of *E. tanala* typically occupy middle montane associations, with most records coming from 800 to 1600 m, whereas those of *E. webbi* inhabit lowland rain forest, usually between sea level and 800 m. Overlap and syntopy of the two have been documented within an altitudinal band from 450 to 875 m (Carleton, 1994; Goodman & Carleton, 1996; Chapter 12).

An immense swath of unsampled territory still exists between Lac Alaotra, the previous northernmost report of *E. tanala*, and the RS d'Anjanaharibe-Sud. Surveys within this region would illuminate the nature of cranial and pelage variation and resolve any taxonomic uncertainty regarding our allocation of the large, white-tailed species.

In rendering this specific identification, we perforce remove exceptional size from the differential diagnosis of *Eliurus ellermani*. At present, we prefer to retain *E. ellermani* as a species, although its distinction from *E. tanala*, if it proves distinct, now rests solely on the possession of a dark tail tuft. By so narrowly amending the diagnosis of *E. ellermani*, the nature of contradictory evidence required to falsify its specific status is made more explicit. Two attendant considerations advise such a conservative course. For one, the type locality of *E. ellermani* was mistakenly located by Carleton (1994), as explained in the next section, and should be revisited to obtain new material. For another, coloration of the distal tail has proven to be a highly reliable trait for discriminating individuals of *E. tanala* and *E. webbi* elsewhere in Madagascar (Carleton, 1994). Also, the presence or absence of a contradistinctive tip is complemented, as with *E. petteri* and *E. grandidieri*, by other cranial differences that serve to separate the species. That is to say, we have not found the combination of cranial features that characterize *E. webbi* in a specimen with a white-tipped tail, except in instances of natural caudal injury and hair regeneration around the stump. Additional
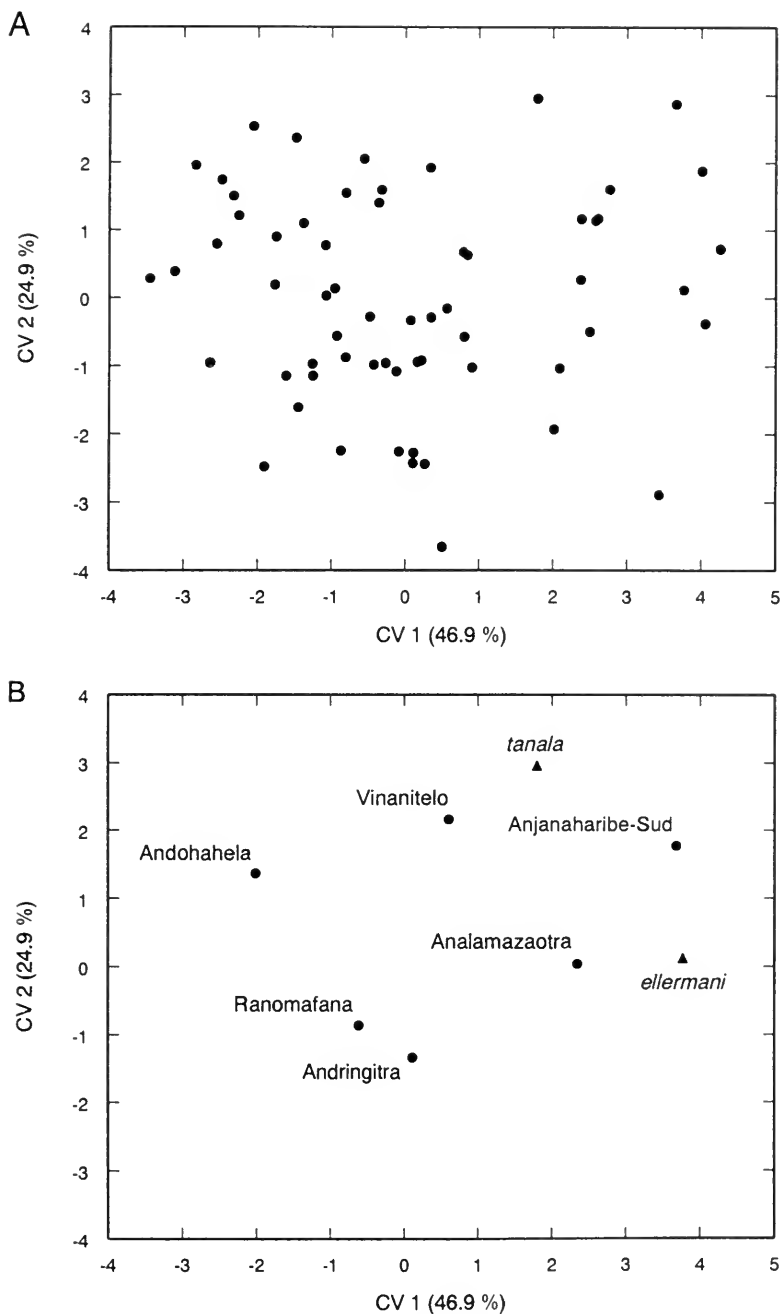
FIG. 11-8.   Results of discriminant function analysis performed on 18 log-transformed craniodental variables, as measured on 62 intact specimens representing six OTUs of *Eliurus tanala*. **Top,** Projection of individual scores onto the first two canonical variates extracted. **Bottom,** projection of OTU centroids onto the first two canonical variates; closed triangles signify the type specimens of *E. ellermani* and *E. tanala.* See Table 11-5 and Figure 11-9.

TABLE 11-5. Results of discriminant function analysis and one-way ANOVA performed on 18 log-transformed craniodental dimensions of 61 specimens representing six OTUs of *Eliurus tanala* (see also Figs. 11-8, 11-9).

Variable	Correlations		F (OTU)
	CV 1	CV 2	
ONL	0.52	0.28	4.3**
ZB	0.35	0.41	3.2*
BBC	0.25	0.53	3.5**
IOB	0.13	−0.06	1.1
LR	0.21	0.14	3.0*
BR	0.50	0.26	3.0*
PPL	0.37	0.19	1.8
LBP	0.38	0.30	4.8**
LIF	0.17	0.16	0.4
BIF	−0.23	−0.71	6.5**
LD	0.40	0.31	3.9**
BM1s	0.40	0.30	2.8*
PPB	0.59	−0.01	5.5***
DAB	−0.10	0.15	1.3
BZP	−0.11	0.39	3.4**
BOC	0.76	−0.10	8.9***
LM1-3	0.30	−0.19	1.6
WM1	0.41	0.24	2.4*
Eigenvalue	3.05	1.0	
Canonical correlation	0.87	0.79	
% Variance	46.9	24.9	

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

collecting at the corrected type locality should answer the question of whether the two specimens that formed the basis of *E. ellermani* are just extreme variants within *E. tanala* or indeed represent a valid species.

TYPE LOCALITY OF *ELIURUS ELLERMANI*—Diagnosis of this form was based on two specimens, the holotype (MNHN 1981.871), collected by R. Albignac at Hiaraka, 850 m, in January 1968, and a paratype (BM(NH) 47.1623), collected by C. S. Webb near Lohariandava, 13 mi (21 km) north of Rogez, 1300 ft (400 m), on 10 December 1939. Carleton (1994) located the type locality Hiaraka as 40 km northwest of Maroantsetra, at approxi-
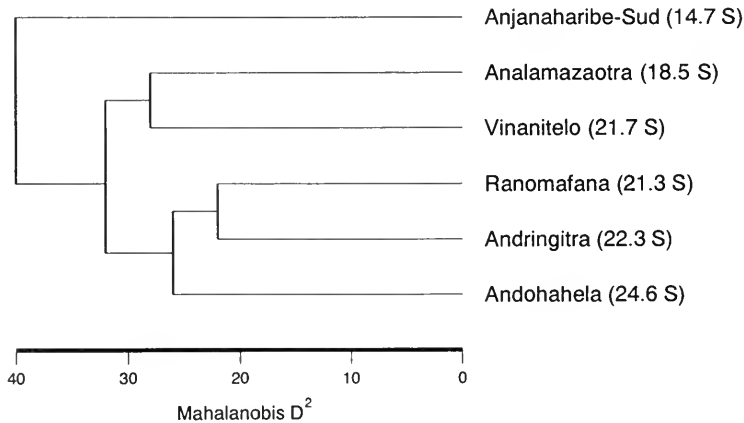
FIG. 11-9. Phenogram produced from clustering (UPGMA) of Mahalanobis' distances among centroids of six population samples of *Eliurus tanala* (degrees of S latitude indicated in parentheses). Associations among samples suggest a gradient in size, from smaller in the south (RNI Andohahela) to larger in the north (RS d'Anjanaharibe-Sud). See also Figure 11-8.

TABLE 11-6. Comparison of selected craniodental measurements for three samples of *Eliurus tanala*.*

Variable	Andohahela 24.6°S (N = 15)	Ranomafana 21.3°S (N = 18)	Analamazaotra 18.5°S (N = 9–16)
ONL	40.4 ± 1.3	41.1 ± 1.5	41.3 ± 1.6
	37.7–42.6	38.5–43.8	38.8–44.1
ZB	19.8 ± 0.7	19.3 ± 0.7	19.8 ± 1.1
	17.6–20.6	18.3–20.6	17.1–21.2
BBC	14.9 ± 0.3	14.7 ± 0.3	14.8 ± 0.3
	14.3–14.9	13.9–15.5	14.4–15.3
IOB	5.8 ± 0.2	5.9 ± 0.3	6.0 ± 0.2
	5.5–6.1	5.6–6.8	5.6–6.4
LR	14.6 ± 0.6	14.8 ± 0.7	14.5 ± 0.8
	13.5–15.5	13.3–15.9	13.4–16.4
BR	7.2 ± 0.3	7.1 ± 0.4	7.4 ± 0.3
	6.6–7.8	6.6–7.8	6.8–7.9
PPL	14.3 ± 0.6	14.4 ± 0.6	14.7 ± 0.8
	12.9–15.2	13.2–15.5	12.9–15.7
LBP	9.3 ± 0.4	9.2 ± 0.4	9.5 ± 0.6
	8.3–9.9	8.2–10.1	8.7–11.0
LIF	5.5 ± 0.3	5.5 ± 0.4	5.5 ± 0.5
	4.9–6.1	4.9–6.1	4.1–6.4
BIF	2.2 ± 0.1	2.4 ± 0.1	2.2 ± 0.2
	2.1–2.4	2.1–2.6	1.9–2.5
LD	12.4 ± 0.5	12.4 ± 0.6	12.7 ± 0.7
	11.2–13.1	11.0–13.6	11.1–13.7
BM1s	7.9 ± 0.2	7.9 ± 0.2	8.1 ± 0.3
	7.5–8.3	7.6–8.6	7.6–8.6
PPB	5.1 ± 0.3	5.3 ± 0.3	5.4 ± 0.3
	4.7–5.7	4.7–5.9	4.7–5.9
DAB	5.4 ± 0.1	5.2 ± 0.2	5.3 ± 0.1
	5.1–5.6	4.9–5.5	4.9–5.5
BZP	4.0 ± 0.2	3.9 ± 0.3	3.8 ± 0.2
	3.5–4.4	3.4–4.7	3.6–4.2
BOC	8.5 ± 0.3	8.6 ± 0.2	9.0 ± 0.2
	7.9–9.0	8.0–9.1	8.7–9.2
LM1-3	5.66 ± 0.22	5.75 ± 0.13	5.80 ± 0.20
	5.17–6.11	5.52–5.99	5.43–6.21
WM1	1.54 ± 0.07	1.53 ± 0.05	1.62 ± 0.09
	1.36–1.64	1.42–1.68	1.43–1.79

* Sample statistics include the mean ± 1 SD and the observed range. See Appendix 11-1 for exact localities and museum numbers.

mately 15°10'S and 49°30'E, following the geographic interpretation of MacPhee (1987).

The place name Hiaraka, however, is a common one in northeastern Madagascar, and we here present information that corrects the type locality erroneously reported for *Eliurus ellermani*. The original tag attached to the skin of MNHN 1981.871 vaguely localizes Hiaraka as "near" Maroantsetra but provides no specific distance. Another nearby Hiaraka is situated on the Masoala Peninsula, just across the Baie d'Antongil from Maroantsetra, about 18 km in an east-southeastern direction. Low mountains, with peaks to 1000–1200 m and with relatively intact forest, occur just inland from this Hiaraka, a small beach enclave currently es-

tablished for tourism. Andre Peyrieras has organized the visits of numerous French biologists to this area, including the 1968 mission of Roland Albignac (Peyrieras, pers. comm.). Hiaraka, located at about 15°30'S and 49°56'E (*sensu* Langrand & Sinclair, 1994), has also been an important locality for insect collecting (Viette, 1991).

Therefore, we amend the type locality of *Eliurus ellermani* Carleton (1994) to the following: Madagascar, Toamasina Province, near Hiaraka, about 18 km ESE of Maroantsetra, 850 m, coordinates about 15°30'S, 49°56'E. Two other species from Hiaraka, as reported by Carleton and Schmidt (1990), were also collected by Albignac in the same general period, an *E. minor* (MNHN

1981.870) in August 1967, no elevation given, and one *Nesomys* [*rufus*] *audeberti* (MNHN 1981.872) in May 1968 at 400 m. With elimination of these records, we cannot reliably associate any nesomyine with the Hiaraka located about 40 km northwest of Maroantsetra, a place also known as Bevato and visited by the Mission Zoologique Franco-Anglo-Américaine (see Archbold, 1930; Goodman, 1995).

The Small *Eliurus*-Like Species

The last issue of taxonomic identity concerns a small, gray, mouselike rodent found in lush, mossy forest at 1950 m just below the summit (Fig. 11-10). Although murine in superficial appearance, examination of the animal's bodily proportions and hindfoot conformation in the field suggested an elfin form of *Eliurus* that lacks a caudal tuft. Subsequent study of its cranium and dentition in the museum revealed other features distinct from those of that genus. Although only three specimens of this small rodent were captured during the 1994 survey of the RS d'Anjanaharibe-Sud, they are sufficient to establish not only that the species is new but also that it does not fit within the morphological limits of any known genus of Nesomyinae.

Voalavo, new genus

TYPE SPECIES—*Voalavo gymnocaudus* Carleton and Goodman, described below as new.

DIAGNOSIS—A form of the murid rodent subfamily Nesomyinae (*sensu* Carleton & Musser, 1984; Musser & Carleton, 1993) characterized by small size (TOTL about 210–215 mm; HB about 86–90 mm) (in other nesomyines except *Monticolomys*, average HB ≥ 100 mm); tail appreciably longer than head and body, TL about 132–138% of HB (TL ≤ HB in *Brachyuromys*, *Gymnuromys*, *Hypogeomys*, and *Nesomys*), without noticeable elongation of caudal hairs over distal half (distal tip penicillate in *Macrotarsomys*, a brushy tuft in *Eliurus*); hindfoot short (HF = 20–21 mm) and relatively broad, outer digits I and V comparatively long (hindfoot long and narrow, outer digits relatively short in *Gymnuromys*, *Macrotarsomys*, and *Nesomys*); hairs of ungual tuft surpassing tip of claw (tuft hairs shorter than claw in *Macrotarsomys*).

Cranium small (ONL = 26–27.5 mm, LM1–3 = 3.7–3.8 mm) and delicately built with slender, nearly parallel sided zygomatic arches and narrow, hourglass-shaped interorbit; zygomatic plate narrow, notch indistinct (plate broader, zygomatic notch shallow to deep in other nesomyines except *Brachytarsomys*); squamosal–alisphenoid bones lacking vascular groove, stapedial and sphenofrontal foramina absent (groove and foramina present in *Macrotarsomys*, *Monticolomys*, and *Nesomys*); alisphenoid strut absent (strut present in *Brachyuromys*, most *Eliurus*, *Hypogeomys*, and *Nesomys*); ectotympanic bullae very small, like *Eliurus*, relatively wide ventromedial wedge of periotic exposed (bullae more inflated, narrow expanse of periotic visible in *Monticolomys*; bullae much larger, periotic mostly obscured in *Brachyuromys*, *Hypogeomys*, *Macrotarsomys*, and *Nesomys*); tegmen tympani reduced, not contacting squamosal (overlap with squamosal in *Brachytarsomys*, *Eliurus*, and *Gymnuromys*).

Entepicondylar foramen of humerus absent (foramen present in all other nesomyine genera except *Brachyuromys*).

Upper toothrows parallel (convergent anteriorly in *Brachyuromys*, divergent anteriorly in *Macrotarsomys* and *Monticolomys*); molars planar, surfaces configured as nearly transverse laminae, and incipiently high-crowned, approaching *Eliurus* (cheek teeth cuspidate and brachyodont in *Macrotarsomys* and *Monticolomys*, moderately hypsodont with distinct cusps in *Nesomys*); upper and lower third molars notably smaller than second molars (size of third molar approximately equal to second in *Brachyuromys*, *Eliurus*, *Hypogeomys*, and *Nesomys*; conspicuously larger than second molar in *Gymnuromys*); two laminae on lower third molar, lamination undefined on upper third molar (three on third molars of most *Eliurus*); mesolophs and mesolophids absent (present in *Gymnuromys* and *Nesomys*); posteroloph absent on upper first molar, present on upper second molar (posterolophs present on unworn M1–3 of *Eliurus*); upper molars with three roots and lowers with two (upper molars four-rooted in *Hypogeomys*).

MORPHOLOGICAL DESCRIPTION—The single known species is described below.

Voalavo gymnocaudus, new species
(Figs. 11-10–11-18, Table 11-7)

HOLOTYPE—Field Museum of Natural History number 154040; skin, skull, and postcranial skeleton of adult male (original number SMG 7081), collected 25 November 1994 by S. M. Goodman.

FIG. 11-10. View of sclerophyllous montane forest at 1950 m, just below the summit of Anjanaharibe-Anivo. Trees in this high mountain zone are typically lower in height and thickly carpeted with mosses and epiphytes. The holotype (FMNH 154040) of *Voalavo gymnocaudus*, new genus and species, was collected in the Sherman live trap pictured here, positioned on a large horizontal limb approximately 3 m above the forest floor. (Photograph by S. M. Goodman.)

TABLE 11-7. Comparison of selected external and craniodental measurements of the holotype (FMNH 154040) and type series of *Voalavo gymnocaudus* with those representative of *Eliurus minor*.*

| Variable | Voalavo gymnocaudus | | Eliurus minor‡ |
	Holotype	Type series†	
TOTL	212.0	212.7 ± 1.1 212.0–214.0	231.5 ± 13.8 214.0–257.0
HB	86.0	87.7 ± 2.1 86.0–90.0	105.7 ± 6.5 95.0–116.0
TL	119.0	119.3 ± 0.6 119.0–120.0	125.5 ± 8.8 110.0–141.0
HF	21.0	20.7 ± 0.6 20.0–21.0	24.0 ± 1.1 22.0–26.0
WT	22.0	22.0 ± 1.5 20.5–23.5	33.5 ± 4.6 25.0–39.0
ONL	26.9	27.0 ± 0.1 26.9–27.1	30.1 ± 0.9 28.7–31.3
ZB	13.8	13.8 ± 0.2 13.7–14.0	15.0 ± 0.4 14.4–15.7
BBC	11.2	11.2 ± 0.1 11.1–11.3	12.0 ± 0.3 11.4–12.5
IOB	4.6	4.5 ± 0.1 4.4–4.6	4.9 ± 0.1 4.7–5.2
LR	9.7	9.3 ± 0.4 8.8–9.7	10.1 ± 0.5 9.2–10.8
BR	5.0	4.9 ± 0.1 4.8–5.1	5.5 ± 0.2 5.1–5.9
PPL	9.8	9.4 ± 0.2 9.3–9.8	10.7 ± 0.4 10.0–11.2
LBP	4.0	4.4 ± 0.3 4.0–4.7	6.2 ± 0.3 5.4–6.6
LIF	4.5	4.2 ± 0.3 3.9–4.5	3.9 ± 0.1 3.5–4.3
BIF	1.6	1.7 ± 0.1 1.6–1.8	2.0 ± 0.1 1.8–2.2
LD	7.5	7.5 ± 0.1 7.3–7.6	8.5 ± 0.3 7.8–9.1
BM1s	5.5	5.5 ± 0.2 5.2–5.7	6.0 ± 0.1 5.8–6.2
DAB	3.9	3.8 ± 0.1 3.7–3.9	4.5 ± 0.2 4.2–4.8
BZP	2.2	2.2 ± 0.05 2.1–2.3	2.5 ± 0.08 2.3–2.6
BOC	6.5	6.3 ± 0.1 6.1–6.5	6.8 ± 0.2 6.4–7.0
LM1-3	3.72	3.73 ± 0.04 3.70–3.79	4.18 ± 0.08 4.05–4.31
WM1	1.09	1.09 ± 0.04 1.04–1.12	1.14 ± 0.05 1.02–1.19

* Sample statistics include the mean ± 1 SD and the observed range.
† For external variables, N = 3 (FMNH 154040, 154041, and 154267); for cranial variables, N = 4 (FMNH 154040, 154041, 154267, and 156162).
‡ Specimens (N = 11–13) from the vicinity of PN de Ranomafana. See Appendix 11-1 for provenance and museum numbers.

Standard measurements (in mm) from the skin tag of the type include TOTL, 212; HB, 86; TL, 119; HF (without claw), 21 (DHF, as measured by M.D.C. with claw, 21.5); EL, 15; and WT (in g), 22.0. The animal is noted as having scrotal testes (7 × 5 mm) with slightly convoluted epididymi-des, and the microhabitat is recorded as "In 'elfin' upper montane forest. Trap 3 m off ground on 28 cm diam. moss-covered limb of tree."

Both skin and skull are in good condition (Fig. 11-12).

TYPE LOCALITY—Madagascar, Province d'Antsi-

| Voalavo | E. minor | E. petteri | E. grandidieri |

Fig. 11-11. Development of caudal pilosity in *Voalavo gymnocaudus* (FMNH 154040; TL = 119 mm), new genus and species, and three species of *Eliurus*, *E. minor* (USNM 449247; TL = 130 mm), *E. petteri* (USNM 341825; TL = 178 mm), and *E. grandidieri*, new species (FMNH 154048; TL = 186 mm). Full lengths of caudal vertebrae are portrayed to the same scale. Note the sparsely furred tail of *Voalavo* and the elaboration of a terminal tuft on that of members of *Eliurus*.

ranana, Réserve Spéciale d'Anjanaharibe-Sud, 12.2 km WSW of Befingitra, 1950 m, 14°44.8'S, 49°26.0'E (as given by the collector).

REFERRED SPECIMENS—Province d'Antsiranana, RS d'Anjanaharibe-Sud, 12.2 km WSW of Befingitra, 1950 m, 14°44.8'S, 49°26.0'E; FMNH 154041: female, skin, skull, and postcranial skeleton, viscera saved; FMNH 154267: male, skull with whole carcass in fluid, western slope, c. 1300 m, 14°46'S, 49°26'E; FMNH 156162: male, skull with carcass in fluid; FMNH 156163: female, whole carcass in fluid.

FMNH 154041 and 154267 were also collected by S. M. Goodman, on 25 and 26 November 1994, as part of the same inventory. FMNH 156162 and 156163 were captured by Franco Andreone,

between 4 and 12 February 1996, as part of a herpetological survey on the western slopes of the same reserve.

DISTRIBUTION—At present only known from montane and sclerophyllous montane forest, 1300–1950 m, in the RS d'Anjanaharibe-Sud.

DIAGNOSIS—As for the genus, above.

MORPHOLOGICAL DESCRIPTION—Fur soft and short (6–7 mm on midrump), relatively thick and finely textured (based on FMNH 154040 and 154041). Cover hairs of dorsum tricolored, with basal band long, four-fifths or more of shaft length, and plumbeous gray, narrow subterminal band pale buffy, and abbreviated tip black; guard hairs thin and black, a little longer than cover fur, unnoticeable except on rump; combined effect of

FIG. 11-12. Dorsal, ventral, and lateral views of the cranium and lateral view of the mandible of the holotype (FMNH 154040; ONL = 26.9 mm) of *Voalavo gymnocaudus*, new genus and species.

upperparts a dusky gray, more brownish gray on sides. Fur over ventral surface, from throat to groin, bicolored, with proximal three-quarters silver gray and tip white; mostly white to bases on chin; overall impression a dark gray ventrum not sharply contrasted with muted tones of dorsum. Mystacial vibrissae medium in length, the longest whiskers reaching the top of the pinnae when appressed to the skin; genal vibrissae small and inconspicuous. Pinnae short and rounded, thinly clothed externally and along rim with dark brown hairs, inner surface mostly naked. Tail long relative to head and body length (TL about 136% of HB), naked in gross appearance over proximal two-thirds and finely haired toward tip (Fig. 11-11); distal section not elaborated as pencil or terminal tuft; undersurface slightly lighter but dorsal–ventral bicoloration indiscernible. Epidermis

of tail gray, some light mottling underneath, scutellation fine, little obscured by hairs except near tip. Caudal hairs fine and short, about 1–2 mm long and spanning about two annulations; dorsal hairs colored deep brown over most of tail length, ventral hairs white to tip, but terminal 20–40 mm invested dorsally and ventrally with fine white hairs. Mammae number 6 (based on FMNH 154041 and 156163), distributed as one postaxial and two inguinal pairs (or one postaxial, one abdominal, and one inguinal pair *sensu* Voss & Carleton, 1993).

Tops of carpals, metacarpals, and phalanges furred in white; toes and most of metatarsus also white, dusky hairs extend over the tarsus and onto the proximal metatarsus; ungual tufts present but sparsely developed, the longest white hairs extending beyond end of claw; palmar and plantar surfaces naked. Palmar surface of manus with five prominent pads, consisting of three nearly contiguous interdigitals and the larger thenar and hypothenar, these approximately equal in size. Hindfoot relatively broad and short (Table 11–7), HF about 23% of HB, with claws on all digits. Outer digit V of hindfoot nearly as long as central digits (II–IV), the tip of its claw reaching to base of claw (ungual phalanx) of digit IV; claw of hallux extends to end of first phalanx of digit II. Plantar surface naked to heel and bearing six large, fleshy pads (Fig. 11-13); interdigital pads 1–4 positioned near one another at base of digits; hypothenar pad round and cushionlike, only slightly smaller than interdigitals and located just behind the level of interdigital 1; thenar also round to oval, situated near middle of tarsus-metatarsus, and a little larger than interdigital pads.

Cranium lightly constructed, delicate in appearance (Fig. 11-12). Rostrum narrow and moderately long (LR about 34% of ONL), tapering forward gradually from nasolacrimal capsules to end of nasals; anterior tips of nasals rounded to slightly pointed, extending beyond premaxillae and overhanging anterior nares; posterior margins blunt, terminating short of posterior limits of rostral processes of premaxillae. Zygomatic plate narrow, its anterior edge straight and set behind nasolacrimal capsule; dorsal notch indistinct; posterior border of plate positioned about equal to plane of anterior root of M1. Zygomatic arches thin and nearly parallel-sided over midportion, broadest at squamosal–jugal junction and weakly converging anteriorly; jugal relatively deep for size of skull, notably long as in other nesomyines, forming most of midspan of arch and distinctly
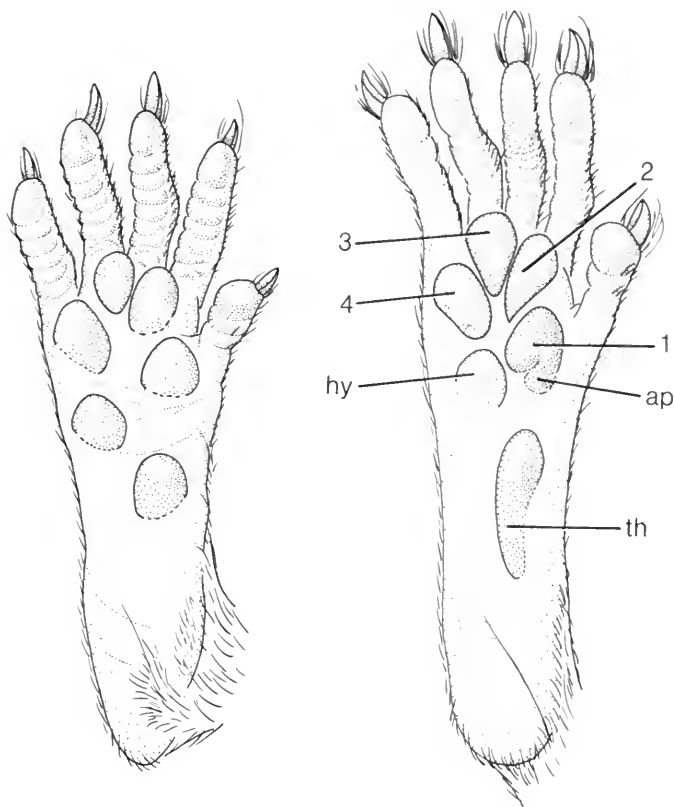
FIG. 11-13. Plantar view of the right hindfoot. **Left,** *Voalavo gymnocaudus* (FMNH 156162: HF = 21 mm), adult male from Antsiranana Province, RS d'Anjanaharibe-Sud. **Right,** *Eliurus minor* (USNM 449388: HF = 22 mm), adult male from Fianarantsoa Province, 3 km NNW of Vohiparara. 1–4 = interdigital pads 1–4; ap = accessory pad on interdigital 1; hy = hypothenar pad; and th = thenar pad. Note especially the contrast in size and shape of the thenar pad between *Eliurus* and *Voalavo*.

separating zygomatic processes of squamosal and maxillary.

Interorbital region short and narrow, exposing floor of orbits in dorsal view; amphoral (hourglass-shaped), lacking supraorbital shelving and ridging; orbital projection of lacrimal small, proportioned as in *Eliurus*. Small rugosity developed on squamosal at rear of orbit, just behind squamosal–frontal suture, forming a low vertical ridge in adult specimens and imparting a squared appearance to anterior braincase. Neurocranium otherwise unmarked by temporal ridges or sagittal crest, smooth and gently rounded at lateral margins; frontoparietal suture defining a 90° angle at midsagittal juncture; interparietal large and wide, rhomboidal in outline but lateral apices not quite contacting squamosals (posterolateral corner of parietal and lateral exoccipital meet narrowly). Dorsal profile of skull conspicuously arched over calvarium, its highest point formed just posterior

to the frontoparietal junction, dorsal profile nearly straight over interorbit and rostrum.

Incisive foramina medium in length, spanning about 55% of diastema and terminating well in front of anterior root of first molars; foramina slightly wider at their midsection, gently convergent at either end but not acutely pointed. Palatal bridge relatively broad and smooth, devoid of corrugations, excrescences, or posteromedial spine; posterior palatine foramina relatively large but occurring as single pair of round to oval holes in maxillopalatine suture, about level with abutment of M1–M2 (foramina large and ovate in holotype, small and circular in others); posterior border of palate broadly rounded, situated even with middle of third molars, and lacking posterolateral palatal pits. Mesopterygoid fossa spacious and horseshoe-shaped; sphenopalatine vacuities wide and long, exposing narrow span of basisphenoid–presphenoid. Parapterygoid fossae slightly broader

than midsection of mesopterygoid fossa, relatively short and triangular in shape, recessed little relative to the plane of the hard palate; roof of parapterygoid fossae almost flat, incompletely ossified with wide fontanelle formed along medial border; fossae also pierced near posterolateral corner by partially occluded opening to alisphenoid canal, which lacks a vascular groove for passage of the infraorbital branch of the stapedial artery.

Ectotympanic bullae small; bullar volume comparable with that of most *Eliurus* species, with large posteromedial wedge of the periotic visible in ventral aspect; mastoid capsule similarly small and bulbous, fully ossified (no posterodorsal fontanelle); malleus typical of the parallel type, with knoblike orbicular apophysis. Tegmen tympani reduced, not overlapping with ventrolateral margin of squamosal; eustachian tube short and wide, not reaching tip of pterygoid process; carotid canal (passage of internal carotid artery) poorly defined as a shallow notch on the rear edge of the eustachian tube. Middle lacerate foramen spacious, its opening confluent with postglenoid foramen; postglenoid foramen medium, semicircular in outline, circumscribing an area about 1.5 times that of the smaller subsquamosal fenestra; hamular process of squamosal well defined and slender.

Alisphenoid strut absent, masticatory–buccinator and accessory oval foramina conjoined as one expansive opening. Sphenofrontal and stapedial foramina absent, vascular imprint lacking across inner surface of squamosal and alisphenoid bones, and posterior opening of alisphenoid canal irregularly formed, anatomical landmarks suggesting a derived carotid circulatory pattern involving loss of the supraorbital and infraorbital branches of the stapedial artery.

Coronoid process of dentary falcate, extending dorsad slightly above the condylar process; sigmoid notch moderately deep and ovate, concave emargination of angular notch unremarkable in size and shape. Alveolus of lower incisor extends posteriorly to level of coronoid process, notably below ventral rim of sigmoid notch; termination evident as slight bulge on ascending ramus but not protruding as capsular process. Superior and inferior masseteric ridges join anteriorly at obtuse angle, at level below anterior root of m1.

Axial skeleton (per FMNH 154040 and 154041) with 13 thoracic, seven lumbar, four sacral (two pseudosacral), and 38–39 caudal vertebrae. First rib articulates only with first thoracic vertebra, not contacting transverse process of seventh cervical. Neural spine of second thoracic vertebra notably the tallest of the thoracic spines. Entepicondylar foramen of humerus absent.

Upper incisors somewhat delicate, asulcate, and nearly orthodont; enamel yellow to pale orange; face of lower incisors ornamented with close-set, parallel longitudinal ridges as in other nesomyines. Upper molar rows more or less parallel; molar crowns incipiently hypsodont, approaching *Eliurus*. Identity of individual cusps lost, occlusal surfaces planar, configured as slightly oblique to nearly transverse laminae; laminae number 3 on upper and lower first and second molars, 2 on lower third molar, laminae undefined on upper third molar; medial enamel connections (mures and murids) between individual laminae absent. First and second molars, both upper and lower, nearly equal in size (length and occlusal area); upper and lower third molars conspicuously smaller, roughly circular in outline, about one-third to one-half the size of the second molars. Three roots on each upper molar and two on each lower molar.

NOTES ON NATURAL HISTORY—All three specimens of *Voalavo gymnocaudus* obtained during the 1994 inventory were collected at the uppermost station of the elevational transect, at 1950 m, just below the summit of Anjanaharibe-Anivo (Fig. 1-1). The habitat at 1950 m may be generally categorized as sclerophyllous montane forest. Tree height in this high mountain zone is typically lower, and bryophytes and epiphytes profusely carpet plant and ground surfaces (Fig. 11-10); such physiognomic and floristic characteristics evoke the other common descriptors of this vegetational community, "elfin" or "mossy" forest. Although little rain fell during the brief visit in late November, the upper slopes around the 1950 m camp were usually shrouded in clouds, and mossy surfaces were drenched with moisture. The 1996 records of *V. gymnocaudus* from the western slopes of the RS d'Anjanaharibe-Sud, around 1300 m, suggest that the species may range more widely over moist montane forest within the reserve and perhaps elsewhere in the highlands of northern Madagascar. The extent of its distribution remains to be learned.

At 1950 m, the three examples of *Voalavo gymnocaudus* were trapped with individuals of *Eliurus majori* and *Nesomys rufus*, as well as the ubiquitous *Rattus rattus*. Its occurrence in montane forest as low as 1300 m indicates probable sympatry with other nesomyines like *E. grandidieri*, *E. minor*, *E. tanala*, and *Gymnuromys roberti*. Additional observations on ecology and re-

productive condition of the few specimens of *Voalavo* obtained are reported in Chapter 12.

ETYMOLOGY—The generic name *Voalavo* is a Malagasy word used generally for "rodent." The epithet *gymnocaudus* draws attention to the animal's apparently naked tail, a trait that readily separates the new genus from its presumed nearest generic ally, *Eliurus*, or tufted-tailed rats.

Morphological Comparisons

Whether indexed by weight or by linear dimensions of the skin and skull, individuals of *Voalavo gymnocaudus* qualify as the smallest form of Nesomyinae so far known, smaller even than *Monticolomys koopmani*, another montane taxon recently described from the Central High Plateau (Carleton & Goodman, 1996). The diminutive size and generalized mouselike appearance easily separate *Voalavo* from the larger, morphologically distinctive forms like *Brachytarsomys*, *Brachyuromys*, *Gymnuromys*, *Hypogeomys*, *Macrotarsomys*, and *Nesomys* (e.g., see descriptions, measurements, and/or keys in Ellerman, 1941, 1949; Petter, 1972, 1975; Carleton & Goodman, 1996; Goodman & Carleton, 1996; and Chapter 12 this volume). Although discrimination of the new genus from most nesomyines is unproblematic, species of *Eliurus* possess several traits that suggest their close affinity to *Voalavo*. Detailed comparison and contrast of these two genera follow.

EXTERNAL FORM—Examples of *Voalavo* and *Eliurus* resemble one another in many aspects of their external appearance and bodily proportions. In view of the pelage variation observed within *Eliurus*, nothing about the texture, color, or degree of dorsal–ventral countershading in *Voalavo* stands apart as inherently different. The genera display the same general foot morphology, including the position and number of pads on the fore- and hindfeet, comparative lengths of the metapodials and phalanges, and presence of ungual tufts. In particular, the development of the fifth toe is comparable in both and approximates the length of the three central digits (Fig. 11-13). Females of *Voalavo* and *Eliurus* possess six mammae, arranged as one postaxial and two inguinal pairs.

The absence of a terminal caudal tuft constitutes visually obvious means for segregating specimens of *Voalavo* from those of *Eliurus*, all species of which exhibit a pronounced elongation of hairs over the distal one-third to one-half of the tail length (Carleton, 1994). Although the tail of *Voalavo* appears almost naked when inspected superficially, careful or microscopic examination reveals a fine cover of short hairs. Near the tip, the caudal hairs lengthen (maximum 1–2 mm long) and may be grossly discernable (Fig. 11-11). As conveyed by their vernacular name, tufted-tailed rats, the distal caudal plume borne by specimens of *Eliurus* is lush and readily discernible, the individual hairs ranging from 8 to 15 mm long, depending on the species. The white hairs and pale epidermis that accent the caudal tip of *Voalavo* also characterize some species of *Eliurus*, such as *E. grandidieri* and *E. tanala*, although the bicolored tips of the latter are more obvious because of the abrupt elongation of distal hairs (Fig. 11-11). The tail of *Voalavo* is long for the size of body (TL about 136% of HB), equal in proportion to the longest known among species of *Eliurus* (namely, *E. grandidieri* and *E. petteri*); however, most *Eliurus* have comparatively shorter tails (115–120% of HB).

A less dramatic but equally consistent generic dissimilarity involves the conformation of the plantar pads of the hindfoot. In members of *Eliurus*, the medial tarsal pad (thenar) is conspicuous among the plantar complement of six, being strikingly longer, obovate in shape, and generally twice the area of the anterior pads; the thenar in examples of *Voalavo* is circular in outline and more or less equal in size to the hypothenar and interdigitals (Fig. 11-13). Small, incompletely formed pads regularly occur at the outer border of the first and sometimes the fourth interdigital pads of *Eliurus* (see also Carleton, 1994: Fig. 2); such subdivisions of the primary interdigital pads are not defined on any individuals of *Voalavo*, including the three fluid-preserved specimens. Although distributed similarly over the plantar surface, the pads of both the manus and pes are larger, more bulbous, and nearly contiguous in *Eliurus*.

CRANIUM AND MANDIBLE—Skulls of *Voalavo* and *Eliurus* are fundamentally alike in proportions and general appearance, their facial skeleton moderately long (LR about 34–36% of ONL), the interorbital region amphoral and devoid of supraorbital ridges, and the braincase smooth and gently contoured. In both genera, a narrow flange of the alisphenoid bone extends dorsally above the level of the orbitosphenoid and contributes appreciably to the rear wall of the orbit. The ventral aspect of their crania displays as many similarities: the palatal bridge in

both is basically flat and featureless, the parapterygoid fossae shallow and equally perforated, and the mesopterygoid fossa wide, enclosing spacious sphenopalatine vacuities. The small ectotympanic bullae of *Voalavo*, their formation relative to the exposure of the periotic and the forward extension of the eustachian tube relative to the pterygoid process, resemble the condition observed in examples of *Eliurus.* The two genera lack certain cranial foramina (stapedial and sphenofrontal) and arterial traces (squamosal–alisphenoid and parapterygoid grooves), which together indicate a derived carotid circulatory pathway (Bugge, 1970; Carleton & Musser, 1989).

In other cranial characters, the condition observed in *Voalavo* matches one state within the array of variation so far documented among species of *Eliurus*. The four crania of *Voalavo* exhibit union of the masticatory–buccinator and accessory oval foramina (strut of the alisphenoid bone missing). Almost all specimens of almost all species of *Eliurus* possess the bony pillar that separates these foramina as discrete openings at the base of the alisphenoid; only the three known examples of *E. petteri* and a few *E. grandidieri* lack an alisphenoid strut. The postglenoid foramen and subsquamosal fenestra, and the bony hamular partition between them, are clearly defined in *Voalavo*; patency of the subsquamosal fenestra and concomitant definition of the hamular process of the squamosal are more variable among species of *Eliurus*, clearly marked in most but nearly occluded in some (especially *E. tanala*). The presence of a rugosity on the rear orbital wall, expressed as a low vertical ridge in fully adult *Voalavo*, is atypical of *Eliurus*, in which the rear orbital wall is usually smoothly contoured. It is common in certain species, however, particularly samples of *E. majori* and *E. minor*, and appears to vary with size and age as with other osseous features associated with muscle origins. By its position and vertical orientation, this rugosity recalls the postorbital ridge described for *Holochilus* (Voss & Carleton, 1993: Fig. 9) but is never so large or pronounced as to obscure the frontosquamosal suture in lateral view. The incisive foramina of *Voalavo* are long relative to the diastemal span, equaling the longest observed within *Eliurus* (*E. majori* and *E. penicillatus*) and clearly exceeding the size characteristic of most species (Fig. 11-14). The lower incisor of *Voalavo* has a relatively short alveolus and correspondingly indistinct capsular process, features that resemble those of certain *Eliurus* (*E. grandidieri, E. majori,* and *E. petteri*); however, most species of the latter genus possess a longer incisor that terminates as a distinct lateral mound just below or at the sigmoid notch.

The regions of the auditory bullae and anterior zygoma present trenchant contrasts between the crania of *Voalavo* and *Eliurus*. The tegmen tympani, an anterior flange of the periotic that roofs the epitympanic recess, continues forward in examples of *Eliurus* to firmly contact the squamosal bone. The margin of the squamosal bows posteroventrally where the lip of the tegmen tympani overlaps, and their articulation forms an osseous division between the openings of the postglenoid and middle lacerate foramina (Fig. 11-15). The tegmen tympani is notably shorter in specimens of *Voalavo*, such that the postglenoid and middle lacerate foramina are broadly confluent. Although the subsquamosal fenestrae remain open in most *Eliurus*, they are typically smaller and cleftlike, exposing the lateral wall of the periotic but none or little of the lumen of the braincase. The hamular process of the squamosal thus appears as a short, stout strut adnate to the mastoid capsule. In the sample of *Voalavo*, the subsquamosal fenestrae are more spacious, revealing the lumen of the braincase and, together with the postglenoid foramen, delineating a slim hamular process (Fig. 11-15).

The configuration of the anterior portion of the zygomatic arch differs substantially (Fig. 11-16). In species of *Eliurus*, the zygomatic plate is uniformly wider, its anterior edge slightly overlapping the nasolacrimal capsule and forming a discrete zygomatic notch. In *Voalavo gymnocaudus*, the plate is narrower and its straight forward edge does not extend beyond the rear margin of the nasolacrimal capsule; accordingly, the anterodorsal rim of the zygoma is scarcely emarginated where the free dorsal edge of the narrow plate meets the superior ramus of the infraorbital canal. Although the zygomatic plate in *Eliurus* is relatively narrow among Nesomyinae, for instance, compared with species of *Brachyuromys* and *Nesomys*, the dorsal notch is nonetheless consistently defined, albeit shallow. Among nesomyines, *Voalavo*, in its rudimentary expression of a notch, surpasses only the construction found in *Brachytarsomys*,
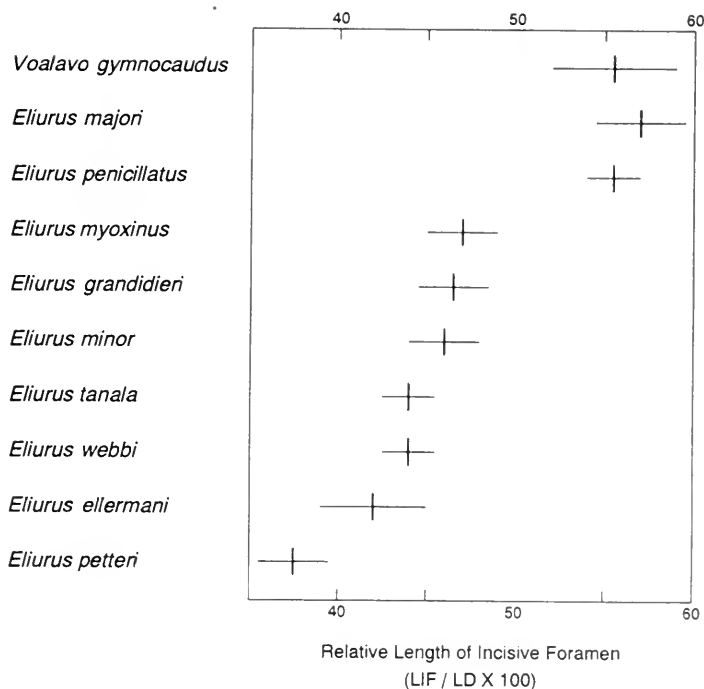
FIG. 11-14.   Relative length of the incisive foramen in *Voalavo gymnocaudus* and species of *Eliurus.* Relative length expressed as the ratio of LIF/LD × 100; the vertical line is the mean of the sample, and the horizontal line corresponds to ±2 standard errors of the mean.

a form that lacks any anterior projection of the zygomatic plate.

DENTITION—The molar topography characteristic of *Voalavo* and *Eliurus* offers several points of similarity suggestive of their near kinship. Compared with the brachyodont teeth of *Macrotarsomys* and *Monticolomys*, their molars are moderately hypsodont, the higher crowns achieved both through vertical elongation of the laminae and the molar bases. The occlusal sur-
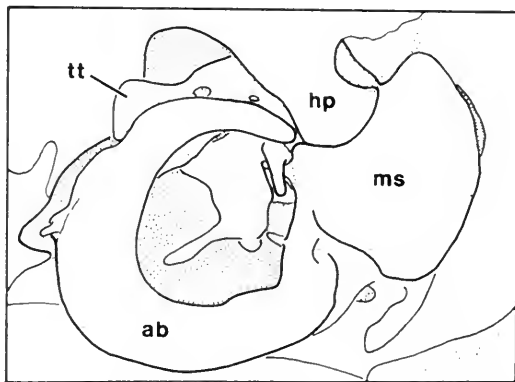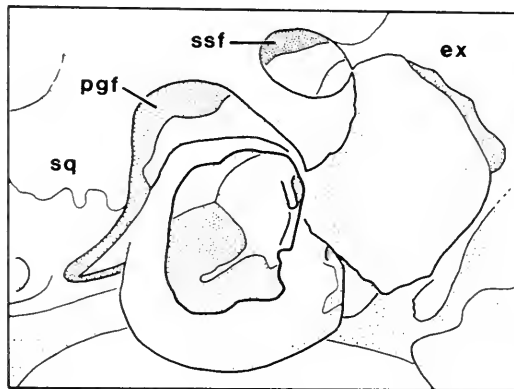
FIG. 11-15.   Left lateral view of the otic region and associated foramina. **Left,** *Voalavo gymnocaudus* (FMNH 156162; Antsiranana Province, RS d'Anjanaharibe-Sud). **Right,** *Eliurus minor* (USNM 449246; Fianarantsoa Province, 3 km NNW of Vohiparara). ab = auditory bulla (ectotympanic); ex = exoccipital; hp = hamular process; ms = mastoid capsule of periotic; pgf = postglenoid foramen; sq = squamosal; ssf = subsquamosal fenestra; and tt = tegmen tympani. The tegmen tympani in members of *Eliurus* strongly abuts the squamosal bone, a connection not observed in *Voalavo.*
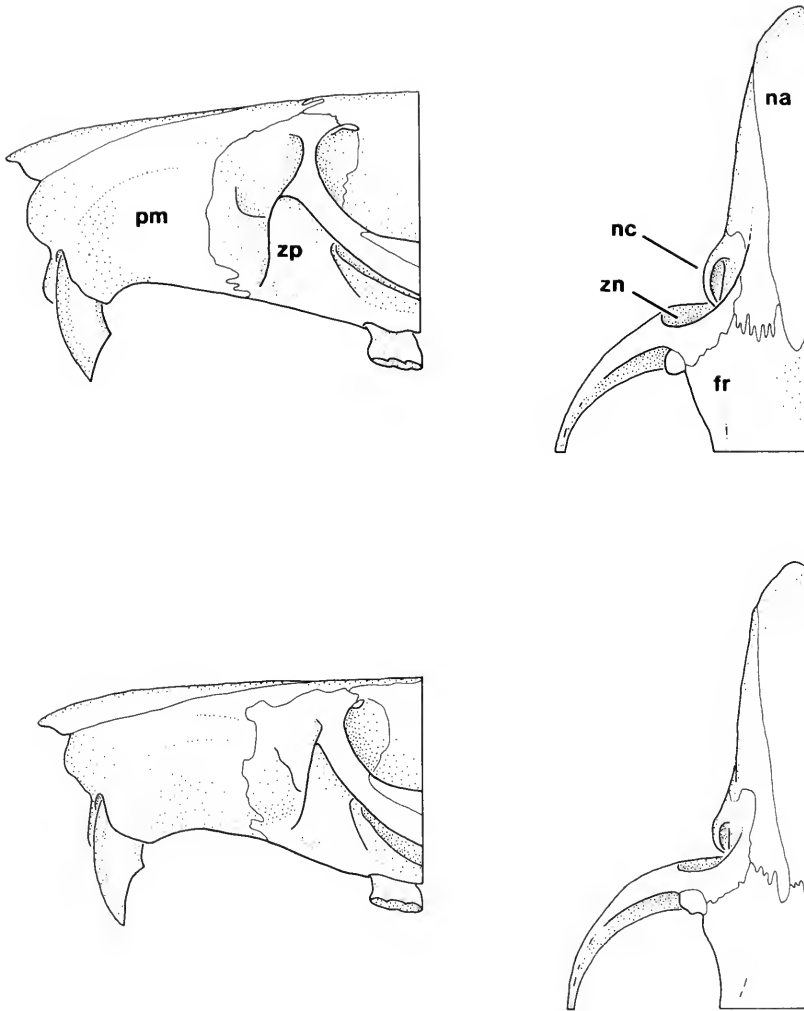
FIG. 11-16. Left lateral and dorsal views of the rostrum and anterior zygomatic region. **Top,** *Eliurus minor* (USNM 449246: Fianarantsoa Province, 3 km NNW of Vohiparara). **Bottom,** *Voalavo gymnocaudus* (FMNH 154041: Antsiranana Province, RS d'Anjanaharibe-Sud). fr = frontal; nlc = nasolacrimal capsule; na = nasal; pm = premaxilla; zn = zygomatic notch; and zp = zygomatic plate. Note the narrower zygomatic plate and indistinct notch in *Voalavo*.

faces are flat and configured as a series of nearly transverse laminae that lack anterior–posterior enamel connections (one exception in *Voalavo*, see below), except at their outer edges with advanced wear. The molar hypsodonty and lamination observed in *Eliurus* and *Voalavo* obscure discernment of cusp homology in formation of the laminae. Notwithstanding precise identification of homologous cusps, the arrangement of the laminae on the first and second molars, both upper and lower, is remarkably alike in the two genera (Fig. 11-17). The resemblance involves both the number of laminae on the anterior molars and the location of enamel folds or islands

on the lower first (metaflexid?) and upper second molars (posteroflexus?). Three roots appear to anchor the upper molars and two anchor the lower molars in both genera.

Aside from their planar surfaces and transverse orientation of enamel structures, the molar dentitions of *Eliurus* and *Voalavo* reveal several prominent differences. The upper and lower third molars of *Voalavo* are noticeably smaller than their anterior counterparts, about one-half the size of the contiguous second molars whether compared in terms of length or area (Fig. 11-17). Among species of *Eliurus*, the third molars either approximately match the second ones (*E.*
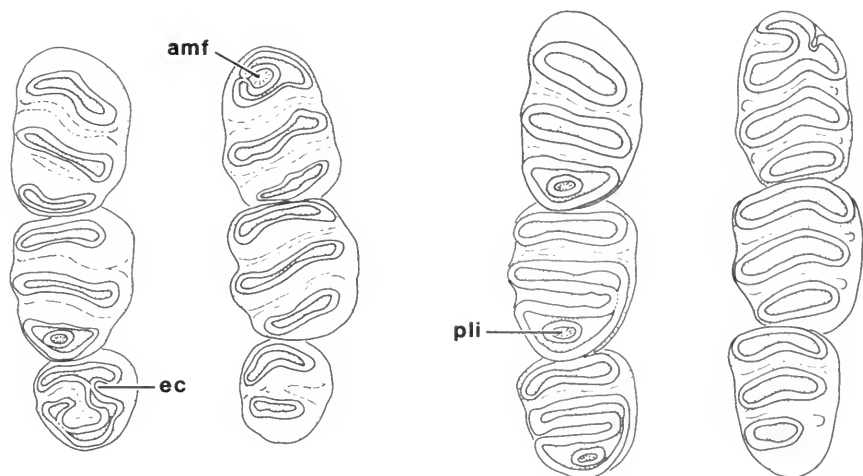
FIG. 11-17.   Occlusal views of the upper (left member) and lower (right member) right molar rows. **Left pair,** *Voalavo gymnocaudus* (FMNH 156162: Antsiranana Province, RS d'Anjanaharibe-Sud). **Right pair,** *Eliurus minor* (USNM 449247: Fianarantsoa Province, 3 km NNW of Vohiparara). amf = anteromedial enamel fold (metaflexid?) of m1; ec = enamel connection (median mure?) of M3; and pli = posterolateral enamel island (posterofossettus?) of M2. Note the smaller third molars in the example of *Voalavo* and the occurrence of only two laminae on its lower third molar in contrast to three in all species of *Eliurus*.

majori and *E. penicillatus*) or attain about two-thirds their size (other species). In *Voalavo*, the lower third molar, perhaps in correlation with its smaller size, bears only two laminae, in contrast to the three uniformly defined on lower third molars of *Eliurus*. Lamination is not at all developed on the upper third molar of *Voalavo*. The small, circular M3 does have a transverse member across its front, perhaps homologous to the first lamina found in *Eliurus*, but the enamel surface of the rear is irregularly formed in the four specimens, usually with interconnected "cusps" surrounding a medial basin. A longitudinal enamel ridge, its position suggestive of a median mure, joins the anterior and posterior sections of M3 in *Voalavo*, whereas such a medial connection is rarely found in *Eliurus*, the first and second laminae being completely segregated by a deep cleft across the width of the tooth. All species of *Eliurus* possess a posterolabial enamel fold (posteroflexus?) at the posterior margin of each upper molar; with slight wear, the fold becomes isolated as an enamel island (posterofossettus?), and with moderate to advanced wear, it becomes entirely obliterated. Only the second upper molar of *Voalavo* exhibits such a fold (Fig. 11-17). Although we characterize the crowns of both *Voalavo* and *Eliurus* as moderately hypsodont, those of the latter genus appear uniformly higher. The descriptive

terminology so far advanced for muroid molar specialization is insufficient to meaningfully discriminate such subtle and graded differences in hypsodonty.

Phylogenetic Relationships

The generic attributes of the seven long-established genera of Nesomyinae—*Hypogeomys* A. Grandidier (1869), *Nesomys* Peters (1870), *Brachytarsomys* Günther (1875), *Eliurus* Milne Edwards (1885), *Brachyuromys* Major (1896b), *Gymnuromys* Major (1896b), and *Macrotarsomys* Milne Edwards and G. Grandidier (1898)—are so sharply marked that hierarchical patterns of kinship among them are obscure. Ellerman's (1941) dissolution of the group indirectly admits this point, although the validity of his reclassification would profit from actual analysis of characters and phylogenetic reconstruction to be sure. However, like the recently diagnosed *Monticolomys* (Carleton & Goodman, 1996), the elfin nesomyine from RS d'Anjanaharibe-Sud represents another instance of a new genus with demonstrable phyletic affiliation with a previously described form, in this case *Eliurus*. In fact, definition of *Voalavo* and *Eliurus* each rests upon their own collection of synapomorphic traits and suggests that the
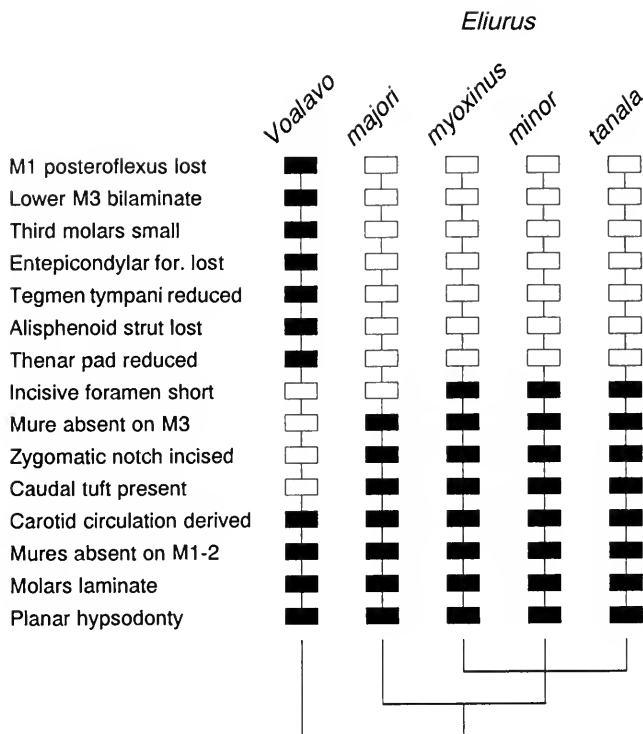
FIG. 11-18. Distribution of presumptive synapomorphies (solid rectangles) and hypothesized cladistic relationship between *Voalavo gymnocaudus*, new genus and species, and representative species of *Eliurus* Milne Edwards (1885). The latter include the type species (*E. myoxinus*), the smallest (*E. minor*) and largest (*E. tanala*) forms within the genus, and a highly differentiated, perhaps cladistically primitive species (*E. majori*).

small eliurine without a caudal tuft is not merely a derivative species of the latter (Fig. 11-18).

Voalavo and *Eliurus* possess several synapomorphic character states that support their near kinship exclusive of other nesomyines. Perhaps the most persuasive among these are certain dental features, such as the nature of their molar hypsodonty, attainment of a planar occlusal surface, and development of lamination. The laminate architecture of their teeth appears to involve the same transverse connections of cusps and attendant loss of accessory crests (mures-ids, mesolophs-ids?), at least for the first and second molars. Evolutionary rearrangement of distal branches of the stapedial artery, mirrored in the loss of certain foramina (stapedial and sphenofrontal) and vascular imprints (squamosal–alisphenoid and parapterygoid grooves), characterizes the skulls of *Voalavo* and *Eliurus*; however, a derived carotid circulation is also common to *Brachytarsomys*, *Brachyuromys*, *Gymnuromys*, and *Hypogeomys*. Other details of morphological agreement between the two—hindfoot conformation, ungual

tufts, interorbital shape, lack of supraorbital shelf and temporal ridging, dorsal extension of the alisphenoid, unremarkable construction of the auditory bullae, and thoracolumbar formula—may be reasonably attributed to symplesiomorphic resemblance. The comparatively elongate incisive foramen typical of *Voalavo* and some *Eliurus* (*E. majori* and *E. penicillatus*) is here interpreted as a primitive condition; polarity for this character, however, is ambiguous when muroids are broadly considered (see Carleton, 1994, for references on divergent viewpoints).

In spite of their morphological similarities, and wanting a full phylogenetic review of the Nesomyinae, generic separation of *Voalavo* and *Eliurus* is defensible on the basis of the association of certain discrete characteristics unique to each. Individuals of *Voalavo* possess several autapomorphies (autapomorphic within our narrow systematic context), involving characters of the foot, cranium, humerus, and molar dentition, that set them apart from *Eliurus* (Fig. 11-18). Generic recognition for the new species *gymnocaudus* does

not leave the diagnosis of *Eliurus* as a paraphyletic construct. The monophyly of that genus is supported by other apomorphies, among them possession of an elaborately penicillate tail, formation of a broader zygomatic plate and distinct notch, and suppression of a mure on the upper third molar. That *Voalavo* retains the plesiomorphic state for each of these three characters suggests that it diverged from a common ancestor before the radiation of tufted-tailed rats, the most speciose of the nesomyine genera.

Biogeography

The inventory of RS d'Anjanaharibe-Sud is the first detailed survey of the rodent fauna of the northern highlands of Madagascar. Earlier work in this region involved only cursory trapping of small mammals and often failed to preserve voucher specimens (e.g., Albignac, 1970; Duckworth & Rakotondraparany, 1990). The discovery of three species of small mammals new to science (see also Chapter 10) based on material obtained in the RS d'Anjanaharibe-Sud underscores how little was known about the fauna of this region.

Elevational transects conducted over the past few years, as well as synthesis of material collected earlier, have provided clearer information on the altitudinal zonation of nesomyine rodents in the eastern humid forest (Carleton & Schmidt, 1990; Carleton, 1994; Goodman & Carleton, 1996; Goodman et al., 1996; Langrand & Goodman, 1997; Chapter 12). In general, most species have well-circumscribed elevational limits that are apparently related to factors associated with vegetational communities. These limits appear to be constant across the latitudinal range of rodent species. The five specimens of *Voalavo gymnocaudus* reported here were taken in two different vegetational zones on the Anjanaharibe-Sud Massif, sclerophyllous forest near the summit at 1950 m and moist montane forest on the western slope at 1300 m.

Judged by paleoecological data from pollen cores taken at several sites on Madagascar (Straka, 1996; Burney, 1997), the distinctive, modern high-mountain vegetational communities descended to approximately 1000 m during certain Quaternary periods when the climate was cooler and drier. Ridges of 1000 m and higher between highland areas would have formed bridges of high-mountain vegetation and provided dispersal corridors for organisms such as *Voalavo*

gymnocaudus. On the basis of such a model, this species should be found to occur broadly across the northern highlands (Fig. 11-19), in regions such as the RNI de Marojejy, the upper zone of the Tsaratanana Massif (2876 m), and satellite peaks to the east and southeast, such as Andramanalana (2260 m) and Biempoko (2219 m). *Voalavo* doubtfully occurs on the Manongarivo Massif, which is separated from these northern highlands by a zone less than 1000 m, or on the isolated Montagne d'Ambre to the far north. The Tsaratanana Massif remains one of most poorly known mountainous areas of Madagascar. Continued zoological exploration of this region will verify whether the proposed model of vegetational shifts can explain the distribution of the high mountain fauna.

Coda

The native rodents of Madagascar have been traditionally characterized as an insular radiation of inordinately low species diversity, an anomaly remarked upon by biogeographers and systematists (Darlington, 1957; Paulian, 1984; Woods & Eisenberg, 1989). The meager diversity of Nesomyinae seemed at odds with Madagascar's size, topographic relief, climatic and floristic complexity, and the ecogeographic opportunities for speciation and phyletic differentiation presumably offered. Certainly, a total of only 10 species, as nesomyine alpha taxonomy was misunderstood for much of the 20th century (following Ellerman, 1949; Petter, 1972, 1975), is conspicuously depauperate compared with rodent assemblages that have populated other large islands occurring within tropical latitudes (Fig. 11-20).

The picture of exceptional impoverishment changed abruptly in the 1990s, a reassessment catalyzed by basic revisionary study and field inventory (Carleton & Schmidt, 1990; Carleton, 1994; Carleton & Goodman, 1996; Goodman & Carleton, 1996; this chapter; Chapter 12). The number of nesomyine species recognized as valid has accordingly doubled in this short interval, elevating the diversity of the subfamily closer to that predicted on the basis of island area (Fig. 11-20). Although recent work has revised upwardly the number of Nesomyinae, the expectation that their specific diversity will match that of rodents on comparably sized tropical islands seems doubtful, even admitting the new forms that will be discov-
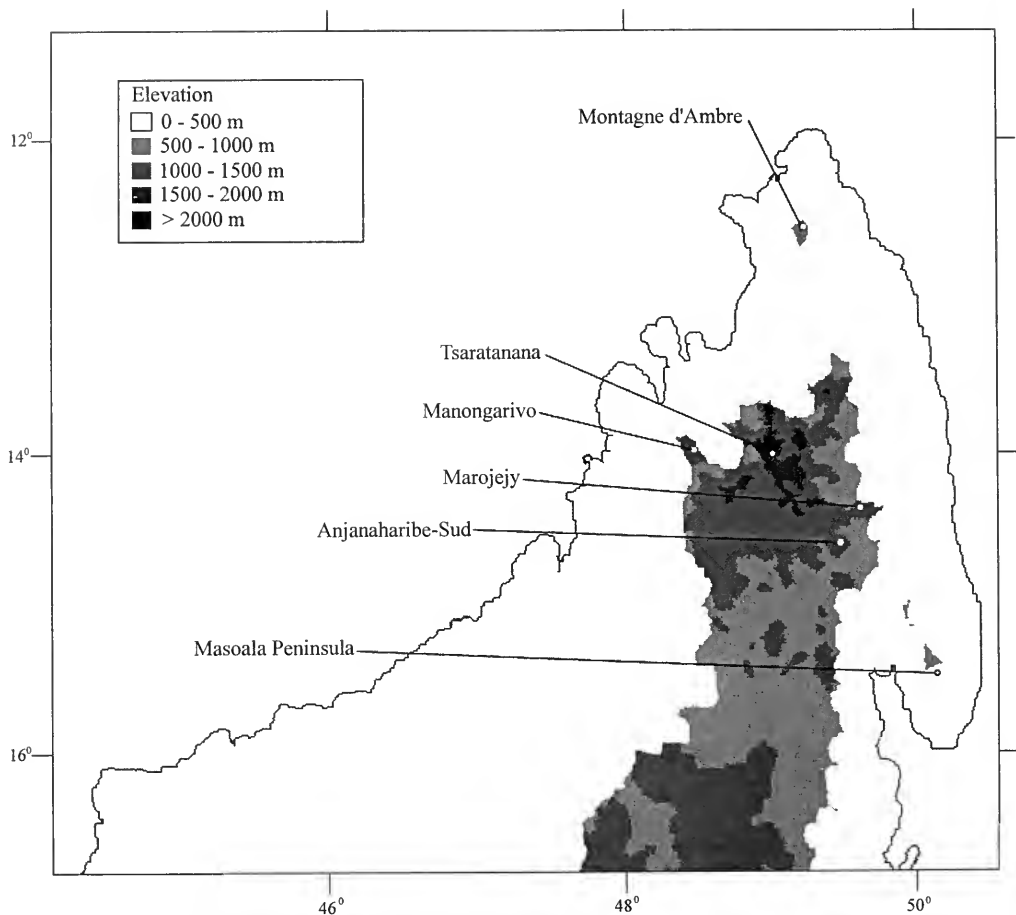
FIG. 11-19. Topographic map of northern Madagascar showing elevational connections between different massifs of the northern highlands.

ered or resurrected from synonymy in the next 5 years. Islands slightly larger than Madagascar, like Borneo and New Guinea, support rodent faunas of 55–60 species (Medway, 1977; Musser, 1987; Flannery, 1995); even islands slightly smaller, like Sulawesi and Sumatra, contain 40–46 species (Heaney, 1986; Musser, 1987). Either range of figures appears unrealistic for Madagascar, based on what has been documented to date and considering what areas have yet to be explored and which genera have yet to be revised.

We anticipate that the trajectory of future research on Madagascar's indigenous species will divulge around 30–35 species. Although not as depauperate as once supposed, considerable difference still exists between this firmer estimate (30–35 species) of Malagasy rodents and that based on the species-area curve derived for other Old World tropical islands (50–55 species). The disparity invites other explanations beyond the mostly correctable artifacts of antiquated taxonomy and insufficient field survey.

Foremost among the biological alternatives is the notion that ecological niches typically filled by rodents were already occupied by an earlier Tertiary radiation of lemurs and tenrecs before the arrival of nesomyines, e.g., as noted by Woods and Eisenberg (1989). The unbalanced faunal composition of nesomyine rodents and strepsirhine primates (32 extant species, *sensu* Mittermeier et al., 1994) attracts immediate attention in comparison with the usual predominance of rodents relative to primate species on other paleotropical islands (4 to 10 times as many; see Carleton & Schmidt, 1990: Table 2). Moreover, several of the Malagasy lemurs, such as *Cheirogaleus* and *Microcebus*, are relatively small-bodied and arboreal, resembling, e.g., the nesomyine *Brachy-*
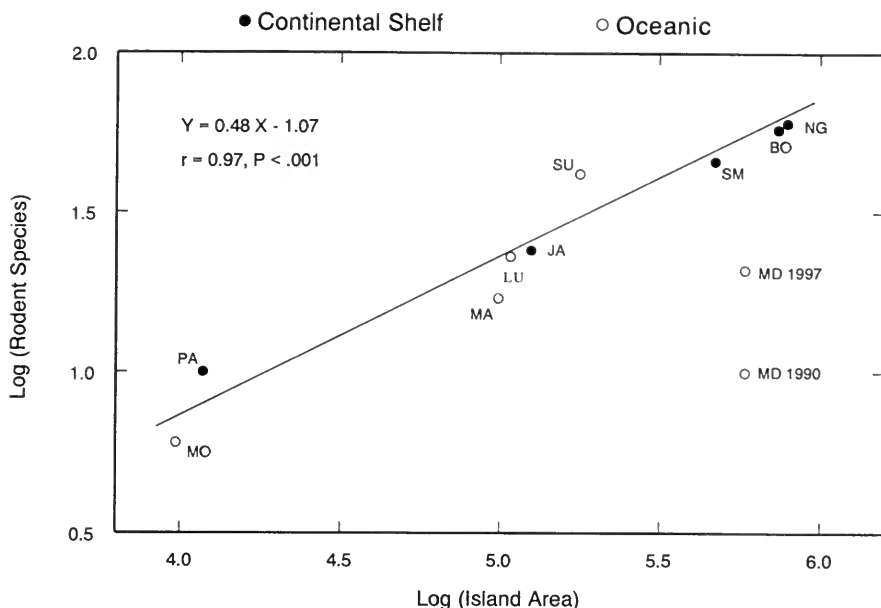
FIG. 11-20. Relationship between log of island area and log of number of indigenous rodent species for large islands with diverse tropical floras. Madagascar was not included in the calculation of the regression statistics (N = 9); see Carleton and Schmidt (1990: Table 2) for island areas, number of rodent species, and literature sources. The intervening years (1990–1997) of taxonomic revision and field exploration have increased the number of indigenous rodent species on Madagascar closer to that predicted on the basis of the island's area (see text for discussion). BO = Borneo; JA = Java; LU = Luzon; MA = Mindinao; MD = Madagascar; MO = Mindoro; NG = New Guinea; PA = Palawan; SM = Sumatra; and SU = Sulawesi.

tarsomys in habits and somewhat in size (see Chapter 12).

Renewed appreciation of the biodiversity of tenrecid insectivores is still emerging, particularly for *Microgale*, with new descriptions and revisions rapidly overturning MacPhee's (1987) improbably low estimate of just 10 species (Jenkins, 1988, 1992, 1993; Jenkins et al., 1996, 1997; Chapter 10). A conspicuous trophic absence among the Nesomyinae, in light of the morphological variety and ecological specializations exhibited by the oryzorictine tenrecs, is the guild of long-snouted, short or long-tailed, small or large-bodied shrew rats and mice. The radiation of murids into such insectivorous and vermivorous niches is commonplace on other tropical islands and archipelagos, such as New Guinea, the Philippines, and Sulawesi (Musser & Freeman, 1981; Musser, 1982, 1987; Flannery, 1995). As currently known, no nesomyine displays such specialized cranial and dental morphologies and the trophic habits they presuppose. Except for the brachyodont, cuspidate molars of *Macrotarsomys* and *Monticolomys*, other nesomyines possess moderate to well-developed hypsodonty (none is hyp-

selodont), and many have prismatic or planar occlusal surfaces with suppression of individual cusps, features that suggest reliance on a herbivorous diet or some mix of granivory and herbivory. With the hydrological sculpting along Madagascar's rugged eastern escarpment, the opportunity for evolution of semiaquatic insectivorous rodents, like those found on New Guinea (Flannery, 1995) and in the Neotropics (Voss, 1988), would seem possible if not likely. Here again, such a semiaquatic habitus on Madagascar was not exploited by nesomyines but is filled by the water tenrec *Limnogale mergulus*.

The applicability of a niche saturation hypothesis, in some form, is worthy of rigorous exploration and firmer argument with regard to the Nesomyinae. Between them, the lemuriform primates and tenrecid insectivores of Madagascar appear to have preempted many ecological niches otherwise filled by rodents in other isolated settings, whether continental (Australia and South America) or insular (New Guinea and Sulawesi) in scale. Another hypothesis, the occurrence of dramatic recent extinctions, associated either with climatic shifts, habitat degradation, or the possible

introduction of hyperdiseases (Burney, 1987; MacPhee & Marx, 1997), remains as intriguing a question for Madagascar's rodents as for its lemurs. A requisite corollary to acceptance of any such explanation, or their combination, is further research on the number and kinds of nesomyine species, their distributions, and their natural histories. The continuing need for investigation of these fundamental sorts hardly bears repetition, nor does restatement of their urgency against the pressures of burgeoning human populations and ever-dwindling natural environments within a fragile insular setting.

Acknowledgments

Literature Cited

ALBIGNAC, R. 1970. Mammifères et oiseaux du Massif du Tsaratanana. Mémoires ORSTOM, **37:** 223–229.

ARCHBOLD, R. 1930. Bevato, a camp in Madagascar. Natural History, **30:** 645–652.

BUGGE, J. 1970. The contribution of the stapedial artery to the cephalic arterial supply in muroid rodents. Acta Anatomica, **76:** 313–336.

BURNEY, D. A. 1987. Pre-settlement vegetation changes at Lake Tritrivakely, Madagascar. Paleoecology of Africa, **18:** 357–381.

———. 1997. Theories and facts regarding Holocene environmental change on Madagascar before and after human colonization, pp. 75–89. *In* Goodman, S. M., and B. D. Patterson, eds., Natural Change and Human Impact in Madagascar. Smithsonian Institution Press, Washington, D.C. xiii + 432 pp.

CARLETON, M. D. 1980. Phylogenetic relationships in neotomine–peromyscine rodents (Muroidea) and a reappraisal of the dichotomy within New World Cricetinae. Miscellaneous Publications of the Museum of Zoology, University of Michigan, **157:** 1–146.

———. 1994. Systematic studies of Madagascar's endemic rodents (Muroidea: Nesomyinae): Revision of the genus *Eliurus*. American Museum Novitates, **3087:** 1–55.

CARLETON, M. D., AND S. M. GOODMAN. 1996. Systematic studies of Madagascar's endemic rodents (Muroidea: Nesomyinae): A new genus and species from the Central Highlands, pp. 231–256. *In* Goodman, S. M., ed., A floral and faunal inventory of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: With reference to elevational variation. Fieldiana: Zoology, n.s., **85:** 1–319.

CARLETON, M. D., AND G. G. MUSSER. 1984. Muroid rodents, pp. 289–379. *In* Anderson, S., and J. K. Jones, Jr., eds., Orders and Families of Recent Mammals of the World. John Wiley and Sons, New York, 686 pp.

———. 1989. Systematic studies of oryzomyine rodents (Muridae, Sigmodontinae): A synopsis of *Microryzomys*. Bulletin of the American Museum of Natural History, **191:** 1–83.

CARLETON, M. D., AND D. F. SCHMIDT. 1990. Systematic studies of Madagascar's endemic rodents (Muroidea: Nesomyinae): An annotated gazetteer of collecting localities of known forms. American Museum Novitates, **2987:** 1–36.

DARLINGTON, P. J. 1957. Zoogeography: The Geographical Distribution of Animals. Wiley Press, New York, xi + 675 pp.

DUCKWORTH, J. W., AND F. RAKOTONDRAPARANY. 1990. The mammals of Marojejy, pp. 54–60. In Safford, R., and Duckworth, J. W., eds., A Wildlife Survey of the Marojejy Nature Reserve, Madagascar. International Council for Bird Preservation, Cambridge.

ELLERMAN, J. R. 1941. The Families and Genera of Living Rodents. Volume 2, Family Muridae. British Museum (Natural History), London, xii + 690 pp.

———. 1949. The Families and Genera of Living Rodents, volume 3, appendix II [notes on the rodents from Madagascar in the British Museum, and on a collection from the island obtained by Mr. C. S. Webb]. British Museum (Natural History), London, v + 210 pp.

FLANNERY, T. 1995. Mammals of New Guinea. Cornell University Press, Ithaca, N.Y. 568 pp.

GOODMAN, S. M. 1995. The third known specimen of the Red-tailed Newtonia *Newtonia fanovanae* (Family Sylviidae), a Malagasy endemic. Bulletin of the British Ornithologists' Club, **115:** 130–132.

GOODMAN, S. M., A. ANDRIANARIMISA, L. E. OLSON, AND V. SOARIMALALA. 1996. Patterns of elevational distribution of birds and small mammals in the humid forest of Montagne d'Ambre, Madagascar. Ecotropica, **2**: 87–98.

GOODMAN, S. M., AND M. D. CARLETON. 1996. The rodents of the Réserve Naturelle Intégrale d'Andringitra, Madagascar, pp. 257–283. *In* Goodman, S. M., ed., A floral and faunal inventory of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: With reference to elevational variation. Fieldiana: Zoology, n.s., **85**: 1–319.

GRANDIDIER, A. 1869. Description de quelques animaux noveaux découverts, pendant l'année 1869, sur la côte ouest de Madagascar. Revue et Magazin de Zoologie, Paris, série 2, **21**: 337–342.

GUNTHER, A. 1875. Notes on some mammals from Madagascar. Proceedings of the Zoological Society of London, **1875**: 78–80.

HEANEY, L. R. 1986. Biogeography of the mammals of SE Asia: Estimates of rates of colonization, extinction, and speciation. Biological Journal of the Linnean Society, **28**: 127–165.

HERSHKOVITZ, P. 1962. Evolution of Neotropical cricetine rodents (Muridae) with special reference to the phyllotine group. Fieldiana, Zoology, **46**: 1–524.

JENKINS, P. D. 1988. A new species of *Microgale* (Insectivora: Tenrecidae) from northeastern Madagascar. American Museum Novitates, **2910**: 1–7.

————. 1992. Description of a new species of *Microgale* (Insectivora: Tenrecidae) from eastern Madagascar. Bulletin of the British Museum Natural History (Zoology), **58**: 53–59.

————. 1993. A new species of *Microgale* (Insectivora: Tenrecidae) from Eastern Madagascar, with an unusual dentition. American Museum Novitates, **3067**: 1–11.

JENKINS, P. D., S. M. GOODMAN, AND C. J. RAXWORTHY. 1996. The shrew tenrecs (*Microgale*) (Insectivora: Tenrecidae) of the Réserve Naturelle Intégrale d'Andringitra, Madagascar, pp. 191–217. *In* Goodman, S. M., ed., A floral and faunal inventory of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: With reference to elevational variation. Fieldiana: Zoology, n.s., **85**: 1–319.

JENKINS, P. D., C. J. RAXWORTHY, AND R. A. NUSSBAUM. 1997. The description of a new species of *Microgale* (Insectivora, Tenrecidae), with comments on the status of four related taxa. Bulletin of the British Museum Natural History (Zoology), **63**: 1–12.

LANGRAND, O., AND S. M. GOODMAN. 1997. Inventaire des oiseaux et des micro-mammifères des zones sommitales de la Réserve Naturelle Intégrale d'Andringitra. Akon'ny Ala, **20**: 39–54.

LANGRAND, O., AND SINCLAIR. 1994. Additions and supplements to the Madagascar avifauna. Ostrich, **65**: 302–310.

MACPHEE, R. D. E. 1987. The shrew tenrecs of Madagascar: Systematic revision and Holocene distribution of *Microgale* (Tenrecidae, Insectivora). American Museum Novitates, **2889**: 1–45.

MACPHEE, R. D. E., AND P. A. MARX. 1997. The 40,000 plague: Humans, hyperdisease, and first-contact extinctions, pp. 169–217. *In* Goodman, S. M., and B. D. Patterson, eds., Natural Change and Human Impact in Madagascar. Smithsonian Institution Press, Washington, D.C.

MAJOR, C. I. FORSYTH. 1896a. Descriptions of four additional new mammals from Madagascar. Annals and Magazine of Natural History, series 6, **18**: 461–463.

————. 1896b. Diagnoses of new mammals from Madagascar. Annals and Magazine of Natural History, series 6, **18**: 318–325.

MEDWAY, L. 1977. The Mammals of Borneo, 2nd edition. Monograph of the Malayan Branch of the Royal Asiatic Society, **7**: 1–172.

MILNE EDWARDS, A. 1885. Description d'une nouvelle espèce de rongeur provenant de Madagascar. Annales des Sciences naturelles, Zoologie et Paléontologie (Paris), **20**: Article 1 bis.

MILNE EDWARDS, A., AND G. GRANDIDIER. 1898. Description d'une espèce nouvelle de Muride provenant de Madagascar. Bulletin du Muséum National d'Histoire Naturelle, série 1, **4**: 179–181.

MITTERMEIER, R. A., I. TATTERSALL, W. R. KONSTANT, D. M. MEYERS, AND R. B. MAST. 1994. Lemurs of Madagascar. Conservation International, Washington D.C., 356 pp.

MUSSER, G. G. 1982. Results of the Archbold expeditions. No. 110. *Crunomys* and the small-bodied shrew rats native to the Philippine Islands and Sulawesi (Celebes). Bulletin of the American Museum of Natural History, **174**: 1–95.

————. 1987. The mammals of Sulawesi, pp. 73–93. *In* Whitmore, T. C., ed., Biogeographic Evolution of the Malay Archipelago. Clarendon Press, Oxford, x + 147 pp.

MUSSER, G. G., AND M. D. CARLETON. 1993. Family Muridae, pp. 501–755. *In* Wilson, D. E., and D. M. Reeder, eds., Mammal Species of the World: A Taxonomic and Geographic Reference, 2nd ed. Smithsonian Institution Press, Washington, D.C., xviii + 1207 pp.

MUSSER, G. G., AND P. W. FREEMAN. 1981. A new species of *Rhynchomys* (Muridae) from the Philippines. Journal of Mammalogy, **62**: 154–159.

PAULIAN, R. 1984. Introduction to the mammals, pp. 151–154. *In* Jolly, A., P. Oberlé, and R. Albignac, eds., Key Environments: Madagascar. Pergamon Press, Oxford, xviii + 239 pp.

PETERS, W. 1870. Uber *Nesomys rufus*, eine neue gattung und art madagascarischer nager. Sitzungs-Berichte der Gesellschaft naturforsender Freunde, Berlin, **1870**: 54–55.

PETTER, F. 1972. The rodents of Madagascar: The seven genera of Malagasy rodents, pp. 661–665. *In* Battistini, R., and G. Richard-Vindard, eds., Biogeography and Ecology in Madagascar. W. Junk, The Hague, xv + 765 pp.

————. 1975. Family Cricetidae: Subfamily Nesomyinae. Part 6.2, pp. 1–4. *In* Meester, J., and H. W. Setzer, eds., The Mammals of Africa: An Identification Manual. Smithsonian Institution Press, Washington, D.C.

REIG, O. A. 1977. A proposed unified nomenclature for the enamelled components of the molar teeth of the

Cricetidae (Rodentia). Journal of Zoology, London, **181**: 227–241.

STRAKA, H. 1996. Histoire de la végétation de Madagascar oriental dans les derniers 100 millénaires, pp. 37–47. *In* Lourenço, W. R., ed., Biogéographie de Madagascar. ORSTOM Editions, Paris.

THOMAS, O. 1895. On a new species of *Eliurus*. Annals and Magazine of Natural History, series 6, **16**: 164–165.

VIETTE, P. 1991. Principales localités où des Insectes ont été recueillis à Madagascar. Faune de Madagascar, supplément 2. Private printing.

VOSS, R. S. 1988. Systematics and ecology of ichthyomyine rodents (Muroidea): Patterns of morphological evolution in a small adaptive radiation. Bulletin of the American Museum of Natural History, **188**: 259–493.

———. 1993. A revision of the Brazilian muroid rodent genus *Delomys* with remarks on "thomasomyine" characters. American Museum Novitates, **3073**: 1–44.

VOSS, R. S., AND M. D. CARLETON. 1993. A new genus for *Hesperomys molitor* Winge and *Holochilus magnus* Hershkovitz (Mammalia, Muridae) with an analysis of its phylogenetic relationships. American Museum Novitates, **3085**: 1–39.

WOODS, C. A., AND J. F. EISENBERG. 1989. The land mammals of Madagascar and the Greater Antilles: Comparison and analysis, pp. 799–826. *In* Woods, C. A. ed., Biogeography of the West Indies: Past, Present, and Future. Sandhill Crane Press, Gainesville, Fla., xviii + 878 pp.

Appendix 11-1.

Comparative Material

Listed below are specimens of *Eliurus* from outside the RS d'Anjanaharibe-Sud that formed the basis for the sample statistics, tabular comparisons, and morphometric analyses presented in the various species accounts. They are contained in the following museums: British Museum (Natural History) (BMNH), London; Field Museum of Natural History (FMNH), Chicago; Merseyside County Museums, Liverpool (LMCM); Museum of Comparative Zoology (MCZ), Harvard University, Cambridge; Muséum National d'Histoire Naturelle (MNHN), Paris; National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.; and Universitets Zoologisk Museum, Copenhagen (UZMC).

Eliurus ellermani—Toamasina Province: Hiaraka, near Maroantsetra, 850 m (MNHN 1981.871, holotype); 13 mi N of Rogez, near Lohariandava, 1300 ft (BMNH 47.1623).

Eliurus minor—Fianarantsoa Province: Ambodiamontana, 7 km W of Ranomafana, 950 m (USNM 448974–448980, 448998); 14 km E of Andraina (USNM 328826); 3 km (by road) NNW of Vohiparara, 1225 m (USNM 449246–449249).

Eliurus myoxinus—Toliara Province: Analabe, 60 km N of Morondava (MNHN 1980.290, 1982.988); Beroboka, 40 mi N of Morondava (BMNH 47.1608, 47.1609, 1987.50); 5 mi E of Bevilany, Ambovombe–Fort Dauphin road, 800 ft (BMNH 47.1600–47.1607, 66.2746); Morondava (MNHN 1973.516); Tsilambana (MNHN 1886.1120, holotype); 35 mi E of Tulear (BMNH 47.1610, 47.1611, 47.1611a).

Eliurus penicillatus—Fianarantsoa Province: Ampitambe (BMNH 97.9.1.148–97.9.1.150, 97.9.1.152, 1939.1892; FMNH 5630, 18822; LMCM A19.4.98.26; MCZ 12435, 45932; MNHN 1897.536, 1909.191; USNM 49672; UZMC 1219, 1224, 7941).

Eliurus petteri—Toamasina Province: 8 km from Fanovana (MNHN 1961.177, holotype); 18 km E of Périnet (USNM 341825); north of Rogez (MCZ 45928).

Eliurus tanala—Fianarantsoa Province: Ambodiamontana, 7 km (by road) W of Ranomafana, 950 m (USNM 448981–448990, 449250–449256); 1 km NW of Andrambovato, 875 m (USNM 449256); RNI d'Andringitra, 38–43 km S of Ambalavao, 810–1625 m (FMNH 151687–151692, 151743, 151744, 151869, 151870, 151873, 151874, 151880, 151881); Vinanitelo, 30 mi S of Fianarantsoa (BMNH 97.9.1.154, holotype; FMNH 5631; MCZ 45690); 3 km (by road) NNW of Vohiparara, 1225 m (USNM 449251–449255). Toamasina Province: 10 mi NW of Lohariandava, 1500 ft (BMNH 47.1573); Périnet, near Moramanga, 3000 ft (BMNH 47.1557, 47.1560–47.1568, 47.1571, 47.1572; MNHN 1961.176); 1 km E of Périnet (USNM 341826); 2 km E of Périnet (USNM 328828, 328829); 13 km E of Périnet (USNM 341827). Toliara Province: RNI d'Andohahela (FMNH 156515, 156519–156521, 156531, 156532, 156628, 156631, 156634–156641).

Eliurus webbi—Fianarantsoa Province: 2 km NE of Andrambovato, 575 and 625 m (USNM 449266–449268); 1 km NW of Andrambovato, 875 m (USNM 449269); 12 km E of Ifanadiana (MNHN 1961.216–1961.219); 0.5 km N of Kianjavato, 300 m (USNM 448991–448995); 9 km ESE of Kianjavato, 250–500 m (USNM 449257–449265).

Chapter 12

The Rodents of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar

Steven M. Goodman[1] **and Michael D. Carleton**[2]

Abstract

In October and November 1994, rodents were studied on the slopes of the Réserve Spéciale d'Anjanaharibe-Sud in four elevational zones between 875 and 1950 m. Nine species belonging to the endemic subfamily Nesomyinae (*Brachytarsomys albicauda, Eliurus grandidieri, E. majori, E. minor, E. tanala, E. webbi, Gymnuromys roberti, Nesomys rufus,* and *Voalavo gymnocaudus*), as well as the introduced *Rattus rattus* (subfamily Murinae), were collected. We present information on distribution, measurements, ecology, and reproduction for each species.

The highest diversity and populations of indigenous rodents were encountered in montane forest at 1260 m (six species), but fewer occurred in lowland moist forest at 875 m (four species) and in sclerophyllous montane forest at 1950 m (three species) near the summit. Except for *Rattus rattus*, no species occurs across the complete elevational range sampled, although two, *Eliurus majori* and *Nesomys rufus,* were found at the three higher sites (1260–1950 m). Two rodent taxa are so far known only from the RS d'Anjanaharibe-Sud, *E. grandidieri* and *Voalavo gymnocaudus,* both newly discovered as part of the survey, and are described in Chapter 11.

Résumé

Au mois d'octobre et de novembre 1994, une enquête sur les rongeurs de quatre zones localisées sur un transect altitudinal réalisé entre 875 et 1950 m le long du versant oriental de la forêt humide sempervirente de la Réserve Spéciale (RS) d'Anjanaharibe-Sud a été réalisée. Neuf espèces de rongeurs appartenant à la sous-famille endémique des Nesomynae (*Brachytarsomys albicauda, Eliurus grandidieri, E. majori, E. minor, E. tanala, E. webbi, Gymnuromys roberti, Nesomys rufus,* et *Voalavo gymnocaudus*) ainsi que l'espèce introduite *Rattus rattus* (sous-famille des Murinae) ont été collectées. Les données relatives à la distribution, aux mesures morphométriques, à l'écologie et à la reproduction de chaque espèces sont présentées.

La plus grande diversité spécifique et les densités de populations les plus élevées ont été constatées dans la forêt d'altitude à 1260 m (six espèces), contre quatre espèces dans la forêt de basse altitude à 875 m et enfin trois dans la forêt sclérophylle proche du sommet à 1950 m d'altitude. A l'exception de *Rattus rattus,* aucune autre espèce ne se rencontre sur l'ensemble du transect altitudinal qui a fait l'objet de cet échantillonnage. Cependant deux espèces, *Eliurus majori* et *Nesomys rufus* ont été trouvées au niveau des trois sites les plus hauts en altitude (1260 à 1950 m). Deux genres de rongeurs étaient jusque là connus de la RS d'Anjanaharibe-Sud auxquels se rajoutent deux nouveaux, *E. grandidieri* et *Voalavo gymnocaudus* découverts au cours de cet inventaire.

[1] Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, IL 60605-2496 U.S.A.
[2] Division of Mammals, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560 U.S.A.

Introduction

The native rodents of Madagascar, as currently understood, comprise a group of 18 species that are classified in the Nesomyinae of a broadly defined Muridae (Carleton & Musser, 1984; Musser & Carleton, 1993; Carleton & Goodman, 1996; Chapter 11). In addition to uncertainty about the monophyly of the Nesomyinae (see discussions in Petter, 1972, 1990; Carleton & Musser, 1984; and Dubois et al., 1996), other major gaps still exist in our biological and systematic knowledge of these indigenous rodents. However, renewal of small-mammal field surveys over the past decade and study of the resulting collections are doing much to fill such voids. Recent investigations of Nesomyinae have covered many aspects of their natural history, geographic distribution and elevational range, and systematics (Nicoll et al., 1988; Carleton & Schmidt, 1990; Barden et al., 1991; Ryan et al., 1993; Stephenson, 1993; Carleton 1994; Goodman & Ganzhorn, 1994; Carleton & Goodman, 1996; Goodman & Carleton, 1996; Goodman & Rakotondravony, 1996; Chapter 11).

This chapter focuses on specimens and associated natural history information gathered during the 1994 inventory of rodents that inhabit slightly disturbed lowland moist forest and primary montane and sclerophyllous forests within the Réserve Spéciale (RS) d'Anjanaharibe-Sud. Special attention is devoted to species richness and relative population densities along the elevational gradient of the inventory, ranging from 875 to 1950 m. Finally, the data reported here are integrated with that from the Réserve Naturelle Intégrale (RNI) d'Andringitra (sampled from 720 to 2450 m), situated near the southern end of the Central High Plateau, and based on Goodman and Carleton (1996), Langrand and Goodman (1997), and Goodman (unpubl. data). Both sites form part of a series of inventories on the montane faunas of the island. The field methods and sampling protocols used in the two studies have been standardized, insofar as possible, to allow direct and more rigorous comparisons between rodents found in these widely distant, mountainous settings.

Previous Work in the Region

To our knowledge nothing has previously been published on the rodents of the RS d'Anjanaharibe-Sud. The only list so far produced for the mammals of this reserve (Nicoll & Langrand, 1989) does not mention rodents. During the Mission Zoologique Franco-Anglo-Américaine (FAA), conducted between 1929 and 1931, a place "one day west of Andapa" was visited, and one specimen each of *Eliurus minor* and *Nesomys rufus* was collected in 1930 (Rand, 1932; Carleton & Schmidt, 1990). That locality was near or perhaps within the present-day boundaries of the RS d'Anjanaharibe-Sud, which was not designated as an official reserve until 1958; the coordinates for the site "one day west Andapa" were estimated by Jenkins (1987) as 14°39'S, 49°22'E. Rand (1936: p. 189) recorded the elevation as 1800 m and captured the majesty of the region:

> Here the country was beautiful. To the north a dark mountain rose; to the south, range after range of mountains stretched away, losing themselves in the bluish haze. . . . It was damp and rained nearly every day that we were there, but it was cool, even chilly at night. . . . There were traces of frost some mornings on the tobacco plants outside the tent. Our camp was situated in hilly country on the edge of a high plateau. Besides the low moss and lichen-draped trees and the forest of taller trees like those found on the forests at lower altitudes, we found open ground stretching away to the west. Each valley had a little swamp with grass or reeds growing in it, and the ridges were covered with low brush, bracken, and grass.

The Mission Zoologique FAA visited other places in the general region of the RS d'Anjanaharibe-Sud, where a few rodents were collected (Carleton & Schmidt, 1990; Carleton, 1994): *Eliurus minor,* 20 km SW of Maroantsetra; *E. webbi,* near Antalaha; *Nesomys audeberti,* 2 days NE of Maroantsetra; and *N. rufus,* on the Tsaratanana Massif to the west. Also, limited information is available for small mammals occurring in the RNI de Marojejy, a reserve located just across the Andapa basin from the RS d'Anjanaharibe-Sud (Duckworth & Rakotondraparany, 1990), but certain specific identifications are ambiguous for want of reference material.

Materials and Methods

This study is based on field work conducted between 16 October and 30 November 1994 by Goodman, who analyzed the trapping results and general ecological data. Carleton refined taxonomic determinations and undertook systematic comparisons.

Field Methods and Trapping Protocol

The general protocol follows that of Goodman and Carleton (1996). At four elevational levels (875, 1260, 1550, and 1950 m), trap lines were maintained for a minimum of 5 nights, and a minimum of 100 traps were installed within each zone (Table 12-1). Each trap line, numbered sequentially starting with the 875 m zone, consisted of Sherman live traps (9 × 3.5 × 3 in.) and National live traps (16 × 5 × 5 in.) in a ratio of 4:1. Traps were baited daily, generally between 15:00 and 17:00 hr, with finely ground peanut butter and ground maize freshly mixed in proportions to make a paste, and lines were inspected at least twice per day, once at dawn and again in late afternoon. Arrays of pitfall traps were also installed in each elevational zone, but these yielded few rodents in comparison to the numerous insectivores (see Chapter 10).

A trap-night is defined as one live trap in use for a 24-hour period (dawn to dawn). The total number of trap-nights accrued at each elevation varied slightly; consequently, the first 500 trap-nights in an elevational zone are considered the "standardized" trapping regimen to facilitate comparisons among the four sites. Standing biomass of a species is based on the total catch of individuals during a standardized trapping regimen multiplied by average body weight of the species (Table 12-2). Instead of an areal factor, population density is calculated as a linear estimate, that is, the number of individuals of a given species obtained per 100 m of trap line within an elevational zone.

The exclusive reliance on live traps during these small-mammal surveys, rather than on a combination of live and snap traps, stems from both the composition of the island's trappable small-mammal fauna and attendant permit restrictions. Significant in this regard is that small primates, such as mouse lemurs (*Microcebus*) and fat-tailed lemurs (*Cheirogaleus*), are relatively common at some sites and readily enter kill traps. The use of live traps allows release of any captured lemurs unharmed.

To quantify differences in spatial distribution of small-mammal captures, several trapping variables were systematically recorded for each trap installed: (1) type of trap, (2) total length of trap line, (3) distance between traps, and (4) specific placement of trap, including its substrate, surrounding forest structure, and position on or height above the ground. Categorization of micro-

habitat location (variable 4) was simplified from the overly detailed system presented by Goodman and Carleton (1996) as follows:

On ground: (1) In leaf litter, generally in area of open understory; (2) under decomposed downed trees or woody vegetation; (3) by tree root or trunk with or without cavity or hole; and (4) miscellaneous, including placement under exposed rocks or boulders, at base of rock face, in thick herbaceous vegetation, and on moss-covered rocks.

Above ground: (1) On liana, limb or trunk less than 10 cm in diameter in horizontal to vertical position; (2) on liana, limb or trunk greater than 10 cm in diameter in horizontal to vertical position; (3) on limbs or trunks suspended by lianas; and (4) miscellaneous, including placement on bamboo stalks, in small cavities at junctions of tree limbs, and on large moss-covered rocks.

Specimens and Measurements

Captured animals were prepared as either standard museum skins with associated skulls and partial skeletons, fluid-preserved carcasses, or full skeletons. Whole carcasses were wrapped in fine cheesecloth before immersion in formalin to prevent loss or mixing of ectoparasites between their specific hosts (see Chapter 6). A large proportion of captured rodents were preserved as vouchers during the survey of the RS d'Anjanaharibe-Sud. This material is housed in the Field Museum of Natural History (FMNH), Chicago, and a representative series has been returned to the Département de Biologie Animale, Université d'Antananarivo (UA). Specimens deposited immediately after the survey in the latter institution have not yet been catalogued and are individually referenced by the collector's field numbers (UA-SMG). To confirm taxonomic identifications, nesomyine holdings in other museums (see Appendix in Goodman & Carleton, 1996) were also consulted, and one or both authors have examined the holotypes of all described forms of Nesomyinae, except for Peters's (1870) *Nesomys rufus*.

Six measurements, in millimeters (mm) or grams (g), were taken by Goodman for each specimen in the flesh; their abbreviations and definitions are given below:

TOTL = total length of body and tail, measured from the tip of the nose to the end of

TABLE 12-1. Summary of trap lines in the RS d'Anjanaharibe-Sud.*

Elevation	No. of traps	Length of line (m)	Mean distance between traps (m)	Mean height above ground (m)
875 m (17–29 October)				
Line 1	100	730	7.6 ± 5.80 (1–30)	1.4 ± 0.59 (0.25–2.5), n = 40
Line 2	50	345	7.1 ± 5.24 (1–24)	1.5 ± 0.76 (0.25–3.0), n = 22
1260 m (4–10 November)				
Line 3	100	520	5.2 ± 3.61 (0.5–23)	1.6 ± 0.55 (0.5–3.0), n = 43
1550 m (17–22 November)				
Line 4	100	396	4.0 ± 1.14 (1–10)	1.5 ± 0.46 (0.25–2.0), n = 39
1950 m (24–29 November)				
Line 5	100	423	4.3 ± 2.29 (0.25–12)	1.9 ± 0.62 (0.5–3.0), n = 32

* Descriptive statistics presented as mean ± SD (range). Each line consisted of National and Sherman live traps in a ratio of 4:1 (see page 203).

the last caudal vertebra (not including terminal hair tuft)

HBL = head and body length, measured from the tip of the nose to the distalmost point of the body (at base of tail)

TL = tail length, measured from the base of the tail (held at right angles to the body) to the end of the last caudal vertebra (not including terminal hair tuft)

HFL = hindfoot length, measured from the

TABLE 12-2. External measurements and sample statistics of adult Nesomyinae rodents from the RS d'Anjanaharibe-Sud.*

Species	TOTL	HBL	TL	HFL	EL	WT
Brachytarsomys albicauda	459	210	240	35	17	205
Eliurus grandidieri	293.4	129.8	161.7	27.7	20.0	52.8
	13.4	12.8	12.3	0.8	1.1	5.5
	275–324	118–185	141–186	26–29	18–22	44.5–67.5
	(n = 19)	(n = 23)	(n = 19)	(n = 23)	(n = 23)	(n = 22)
Eliurus majori	354.4	158.7	186.6	29.3	18.8	94.2
	11.4	3.4	8.9	1.1	0.9	10.5
	330–370	155–165	170–202	27–31	18–20	78–109
	(n = 11)	(n = 11)	(n = 11)	(n = 11)	(n = 11)	(n = 10)
Eliurus minor	244.0	110.4	127.8	22.1	16.9	36.9
	17.0	4.4	14.6	0.8	1.0	4.1
	205–260	105–116	94–139	21–23	15–18	31.0–43.5
	(n = 8)	(n = 7)	(n = 8)	(n = 8)	(n = 8)	(n = 7)
Eliurus tanala	361.5	167.8	187.2	33.3	23.2	105.9
	16.1	4.3	17.3	0.5	0.8	12.0
	342–381	163–174	158–203	33–34	22–24	96.5–120
	(n = 4)	(n = 5)	(n = 5)	(n = 4)	(n = 5)	(n = 5)
Eliurus webbi	309.7	142.0	163.5	27.7	23.0	71.9
	14.4	4.8	10.1	1.5	1.6	5.9
	294–332	138–149	153–179	26–29	20–25	63.5–78.5
	(n = 6)	(n = 4)	(n = 6)	(n = 6)	(n = 7)	(n = 6)
Gymnuromys roberti	402, 402	177, 186	210, 212	38, 39	21, 22	141, 170
Nesomys rufus	348.7	183.4	161.3	44.3	26.6	160.8
	9.0	6.1	6.1	1.5	1.1	17.3
	334–361	169–191	154–174	41–46	24–28	128–190
	(n = 12)	(n = 12)	(n = 12)	(n = 12)	(n = 12)	(n = 12)
Voalavo gymnocaudus	212.7	87.7	119.3	20.7	15.0	22.0
	1.2	2.1	0.6	0.6	0.0	1.5
	212–214	86–90	119–120	20–21	15–15	20.5–23.5
	(n = 3)	(n = 3)	(n = 3)	(n = 3)	(n = 3)	(n = 3)

*Values presented are mean, SD, range, and number. See text (pp. 203–205) for definitions of measurement abbreviations.

heel to the tip of the longest toe (not including claw)

EL = ear length, from the basal notch to the distalmost tip of the pinna.

WT = weight, measured in grams with Pesola spring scales to within ±0.5 g for animals less than 100 g and to within ±1.0 g for those between 101 and 300 g.

Sixteen cranial and two dental dimensions were measured by Carleton to the nearest 0.1 mm using handheld digital calipers accurate to 0.03 mm. These measurements, and their abbreviations, follow the anatomical landmarks defined and illustrated in Carleton (1994):

BBC = breadth of the braincase
BIF = breadth of incisive foramina
BM1s = breadth of the bony palate across the first upper molars
BOC = breadth across the occipital condyles
BR = breadth of rostrum
BZP = breadth of the zygomatic plate
DAB = depth of the auditory bulla
IOB = interorbital breadth
LBP = length of bony palate
LD = length of diastema
LIF = length of the incisive foramina
LM1-3 = coronal length of maxillary tooth row
LR = length of rostrum
ONL = occipitonasal length
PPB = posterior breadth of the bony palate
PPL = postpalatal length
WM1 = width of the first upper molar
ZB = zygomatic breadth

Standard descriptive statistics (mean, range, and SD) were derived for adult specimens in each species sample. We define "adult" as those animals that lack the finer, juvenile pelage and that possess fully erupted, although sometimes unworn, third molars. Where sample sizes permitted, two-sample t tests and one-way analyses of variance were applied to the mensural variables, with sex as the categorical variable. Analytical routines were carried out using Systat (version 6.01, 1996). Mammae formulae are presented as the number of paired postaxial, abdominal, or inguinal teats.

Species Accounts

Within each account, field observations and natural history data are presented under the sub-headings "Distribution," "Ecology and Reproduction," "Comments" (as necessary), and "Specimens Examined." For identification criteria and taxonomic discussion, see Carleton (1994), Goodman and Carleton (1996), and Chapter 11. External measurements and weights, however, are provided for the 10 species, both as a practical key and as background reference to the size and mass differentials that characterize the rodent guild of the RS d'Anjanaharibe-Sud.

Family Muridae: Subfamily Murinae

Rattus rattus (Linnaeus, 1758)

DISTRIBUTION—The black rat was captured in all elevational zones sampled throughout the reserve. Elsewhere on the island, wherever surveyed, it seems to occur in remaining stands of pristine eastern humid forest (Goodman, 1995; Goodman & Carleton, 1996).

ECOLOGY AND REPRODUCTION—*Rattus* was most common at 1550 m, where 15 individuals were captured in 500 trap-nights, as compared with the 875, 1260, and 1950 m zones, where only one or two individuals were obtained during each 500 trap-nights of effort (Fig. 12-1). The Andringitra transect, conducted between 720 and 2450 m, within habitats ranging from lowland to sclerophyllous forests (tree line at about 2000 m) through high mountain meadows and the open rocky summital zone (Goodman & Carleton, 1996; Langrand & Goodman, 1997; Goodman, unpubl. data), found a parallel midelevational increase in *R. rattus* densities as in the RS d'Anjanaharibe-Sud (Fig. 12-1). At Andringitra, more *R. rattus* were captured in the 1210 and 1625 m zones than in areas of the mountain above or below this zone.

The 875 m camp was a few kilometers from several small settlements and cleared areas of *tavy*. Such human activities would presumably attract *Rattus rattus* as a commensal animal, yet only one individual was captured in 1,000 trap-nights at this transect. *Rattus* does not appear to be more common in disturbed forest close to human habitation in the RS d'Anjanaharibe-Sud, contrary to the situation in some other Old World tropical countries (Musser, 1987; Heaney et al., 1989).

Seventeen of 19 (89%) *Rattus rattus* captured within the RS d'Anjanaharibe-Sud were trapped on the ground, particularly by roots and trunks (Table 12-3). The other two individuals were
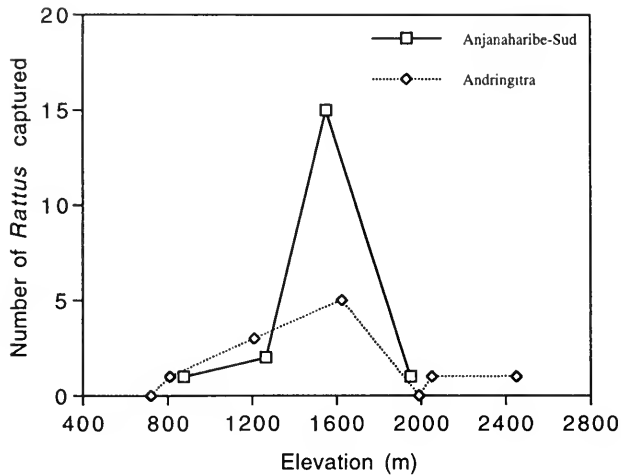
FIG. 12-1. Number of *Rattus rattus* captured at different elevational zones in the RS d'Anjanaharibe-Sud (squares) and the RNI d'Andringitra (diamonds) using similar trapping regimens. The trap success within each elevational zone is standardized at 500 accrued trap-nights. The Andringitra data are based on Goodman and Carleton (1996), Langrand and Goodman (1997), and Goodman (unpubl. data).

taken in sets placed above ground, on limbs and tree trunks at least 10 cm in diameter. The predominantly terrestrial sphere of *Rattus* activity conforms to results obtained in the RNI d'Andringitra, where 64% of black rats were captured in traps set on the ground.

The vast majority of *Rattus rattus* collected were adults. Of the 14 specimens preserved, eight (57%) were scrotal males, one was a male with abdominal testes, three were adult females with large mammae, and two were subadult females with small mammae and imperforated vaginas. The mammae formulae varied among the four females (3-0-1, 1-2-2, 1-2-1, and 2-1-2).

COMMENTS—The history of the introduction and subsequent colonization of Madagascar by *Rattus rattus* is poorly known. As currently documented, the earliest presence of commensal rats on the island dates from 11th to 14th century middens excavated at the Islamic site of Mahilaka, near Ambanja (Rakotozafy, 1996; Radimilahy, 1997). Presumably, rats were transported to Madagascar by Arab traders during this period.

By the close of the 19th century, *Rattus* was already found in numerous remote sites in the eastern humid forest. In 1895 and 1896, Forsyth Major collected *R. rattus* at Ampitambe (BM(NH) 97.9.1.156) and Vinanitelo (BM(NH) 97.9.1.157 and 97.9.1.158), although he made no mention of these captures in his expedition summary (Major 1896a). In the forest in and around the RS d'Analamazaotra, the earliest vouchered record of

R. rattus is a specimen obtained in May 1916 (MNHN 1983.941); by 1939, *Rattus* had colonized the reserve and surrounding forest and "multiplied at an alarming rate," according to Webb (1954: p. 256).

Recent field work has revealed that *Rattus rattus* is a common to abundant member of the small-mammal community and is broadly distributed, geographically and altitudinally, in secondary to pristine humid forest throughout the island (Goodman, 1995; Goodman & Carleton, 1996). The overwhelming abundance of *R. rattus* at certain sites far exceeds the native nesomyines (Goodman et al., in press) and raises concerns that introduced rats are displacing the indigenous small mammals of Madagascar.

No *Rattus norvegicus* were found within the reserve, but a dead individual was discovered in the nearby village of Befingitra.

SPECIMENS EXAMINED—6.5 km SSW of Befingitra, 875 m (UA-SMG 6864); 9.2 km WSW of Befingitra, 1260 m (FMNH 154275; UA-SMG 6983); 11.0 km WSW of Befingitra, 1550 m (FMNH 154039, 154278, 154279, 154280, 154281, 154282, 154283, 154284; UA-SMG 7043); 12.2 km WSW of Befingitra, 1950 m (FMNH 154293).

Family Muridae: Subfamily Nesomyinae

***Brachytarsomys albicauda* Günther, 1875**

DISTRIBUTION—*Brachytarsomys albicauda* is recorded from various localities broadly scattered

TABLE 12-3. Microhabitat occurrences of rodent species by elevation in the RS d'Anjanaharibe-Sud.

Elevation and species	No. taken	Trap position On ground	Trap position Above ground	Ground location* Leaf litter	Ground location* Under rotten wood	Ground location* By roots, trunks	Ground location* Misc.	Above-ground location Vine, limb, or trunk <10 cm	Above-ground location Limbs, trunks >10 cm	Above-ground location Suspended trunks	Above-ground location Misc.
875 m											
Trap distribution†		60	40	11	12	36	1	22	13	3	2
Rattus rattus	1	1				1					
Eliurus minor	1		1					1			
Eliurus webbi	4		4					2	2		
1260 m											
Trap distribution		61	39	7	12	35	7	23	16		
Rattus rattus	2	1	1			1			1		
Eliurus grandidieri	23	19	4	2	3	11	3	1	3		
Eliurus majori	6	1	5	1				2	3		
Eliurus minor	6	1	5			1		2	3		
Eliurus tanala	6	5	1			1	4				1
Gymnuromys roberti	1	1				1					
Nesomys rufus	8	8			2	6					
1550 m											
Trap distribution		60	40	8	13	36	3	21	10	1	8
Rattus rattus	15	14	1		1	13			1		
Eliurus grandidieri	1	1			1						
Eliurus majori	2		2					1	1		
Nesomys rufus	3	3				3					
1950 m											
Trap distribution		66	34	7	7	49	3	12	16		6
Rattus rattus	1	1			1						
Eliurus majori	4		4					1	3		
Nesomys rufus	4	4				3	1				
Voalavo gymnocaudus	3	2	1		1	1			1		
Totals (875–1950 m)											
Trap distribution		247	153	33	44	156	14	78	55	4	16
Rattus rattus	19	17	2		2	15			2		
Eliurus grandidieri	24	20	4	2	4	11	3	1	3		
Eliurus majori	12	1	11	1				4	7		
Eliurus minor	7	1	6			1		3	3		
Eliurus tanala	6	5	1			1	4				1
Eliurus webbi	4		4					2	2		
Gymnuromys roberti	1	1				1					
Nesomys rufus	15	15			2	12	1				
Voalavo gymnocaudus	3	2	1		1	1			1		
Total	89	60	29	3	9	42	6	10	18		1

* See page 203 for habitat definitions.
† Restricted to first 500 trap-nights of line 1.

across the eastern humid forest of the island, over an elevational range of 450–1300 m, from the Sihanaka Forest around the Lac Alaotra region to as far south as Vinanitelo in the vicinity of Fianarantsoa (Carleton & Schmidt, 1990). The record of this species within the RS d'Anjanaharibe-Sud thus extends its known range about 320 km farther north.

ECOLOGY AND REPRODUCTION—People from villages neighboring the reserve mentioned that a large nocturnal and arboreal rodent lives in the forest. They recounted its unusual mode of locomotion, how it inhabits tree hollows, and how, when disturbed, particularly during the day, it sticks its head outside the cavity and utters a chattering sound. Their careful description undoubt-

edly fits the behavior and form of *Brachytarsomys albicauda,* a single specimen of which was captured in the 875 m zone.

The individual had entered a National trap baited with dried coconut and set apart from the standardized small-mammal trap line. The trap was placed on a horizontal portion of a canopy vine, about 3 cm in diameter and 1.5 m above the ground. The vine made a complete loop from an entanglement near midcanopy, down to within 1.5 m of ground, and then back up. The animal was an adult female with large mammae (1-0-2) and was carrying embryos (four in the left uterine horn and two in the right); the crown–rump length was about 21 mm. Lactation tissue had started to form. During specimen preparation it was striking how thick and durable the skin was in comparison with other nesomyine rodents and how much connective tissue was attached to the inner surface of the skin.

When moving about vines and branches of the subcanopy, this arboreal and nocturnal rodent, with its slow-climbing locomotion, is reminiscent of fat-tailed lemurs (*Cheirogaleus*). Furthermore, it is reported to feed mainly on fruits (Petter, 1972). At 875 m on the Anjanaharibe-Sud Massif, *Brachytarsomys albicauda* coexists with a variety of arboreal nocturnal lemurs, including *C. major, Microcebus rufus, Allocebus trichotis, Avahi laniger, Lepilemur mustelinus,* and *Daubentonia madagascariensis* (see Chapter 14). It would be fascinating to investigate aspects of food resources and nesting sites commonly used by *Brachytarsomys* and nocturnal lemurs.

Specimens Examined—6.5 km SSW of Befingitra, 875 m (FMNH 154055).

Eliurus grandidieri Carleton and Goodman, 1998

Distribution—This newly described species (see Chapter 11) is so far known only from middle to upper montane slopes (1260 and 1550 m) in the RS d'Anjanaharibe-Sud. In view of its elevational occurrence in the reserve, it may be expected to occur on the nearby Tsaratanana and Marojejy massifs.

Ecology and Reproduction—At 1260 m, *Eliurus grandidieri* was the most common species of mammal captured, accounting for 23 (47%) of the 49 rodents found in the standardized trap lines. The majority (19 of 23) were taken on the ground; of these, most (11 of 19) were captured near tree roots or trunks, and the remainder were captured in a variety of microhabitats, such as under rotten and fallen tree trunks (three), in areas of open understory with relatively thick leaf litter (two), and at openings under large boulders (three). The dispositions of the arboreal sets that yielded four *E. grandidieri* were as follows: 0.5 m off the ground on the base of an inclined tree trunk (20 cm diameter, 40° slope); at 2 m height, on an arched tree trunk (25 cm diameter); 0.5 m up a moss-covered vine (3 cm diameter) that reached from the ground to lower canopy and back down; and on a horizontal moss-covered tree trunk (14 cm diameter), 1.5 m above the ground. The single individual from the 1260 m zone was trapped on the ground, at the opening of a large hole passing under a tree root and covered with debris.

Animals from the 1260 m zone varied considerably in breeding condition, with four males having scrotal testes and six having abdominal or partially descended testes and with nine females possessing enlarged mammae (one individual lactating) and seven having undeveloped mammae. The single individual from 1550 m was adult, its mammae large, with single embryos (10 mm crown–rump length) present in both the left and right arms of the uterus. The mammae formula, as counted in 16 females, was uniformly 1-0-2.

Specimens Examined—9.2 km WSW of Befingitra, 1260 m (FMNH 154046, 154047, 154253–154257, 154259–154265, 154288, 154290, 154291, 154292; UA-SMG 6913, 6936, 6937, 6944-6946, 7002, 7006); 11.0 km WSW of Befingitra, 1550 m (FMNH 154048).

Eliurus majori Thomas, 1895

Distribution—The elevational range of this species within the reserve is 1260–1950 m, a middle to upper montane setting in accordance with the altitudinal transect performed in the RNI d'Andringitra (Goodman & Carleton, 1996).

As of only a few years ago, *Eliurus majori* was known from only four specimens from three widely separated places: Montagne d'Ambre (1000 m), an isolated peak at the northernmost end of Madagascar; Ambohimitombo (1200 m), the type locality on the eastern edge of the Central High Plateau; and Anjavadilava (2000 m), a place on the Andringitra Massif at the southern end of the Central High Plateau (Carleton, 1994). The relatively common status of *E. majori* in the RS d'Anjanaharibe-Sud indicates that the species may

be more generally distributed than previously thought and that it should be sought in other suitable highland regions of eastern Madagascar.

ECOLOGY AND REPRODUCTION—As in the RNI d'Andringitra, the majority of *Eliurus majori* captured in the RS d'Anjanaharibe-Sud were taken off the ground (Table 12-3). Eleven of 12 individuals captured during the standardized trapping regime were found in sets affixed to vines, limbs, and trunks, all within 3 m of the ground. Of these 11, four had entered traps placed on substrates less than 10 cm in diameter, and seven had entered traps placed on substrates greater than 10 cm in diameter. The single individual trapped on the ground was at the base of a massive tree with a hollow base.

Among the 14 *Eliurus majori* collected were five adult males with scrotal testes, four males with abdominal testes, four adult females with enlarged mammae, and one adult female with small mammae. A lactating female contained three placental scars, but no other females with large mammae showed signs of lactation. The mammae formula was consistently 1-0-2 (n = 4).

SPECIMENS EXAMINED—9.2 km WSW of Befingitra, 1260 m (FMNH 154052, 154241, 154242, 154243, 154258, 154266; UA-SMG 6981, 6998); 11 km WSW of Befingitra, 1550 m (FMNH 154053, 154244); 12.2 km WSW of Befingitra, 1950 m (FMNH 154054, 154245, 154289; UA-SMG 7090).

Eliurus minor Major, 1896b

DISTRIBUTION—*Eliurus minor* has been previously collected at a site "1 day W of Andapa" (Carleton, 1994), which is in or around the RS d'Anjanaharibe-Sud. *Eliurus minor* was found only in the two lower elevational zones at 875 and 1260 m, and information on relative trap success indicates that it was more common in the latter zone. On other mountains in the eastern humid forest, this species has a broad elevational range within the forested zone. For example, in the RNI d'Andringitra, it occurred from 720 to 1625 m, although more individuals were trapped at lower elevations (Goodman & Carleton, 1996).

ECOLOGY AND REPRODUCTION—Of seven *Eliurus minor* captured in the standardized small-mammal trap lines, one was on the ground, and the remainder were in trap sets placed off the ground. The six arboreal captures were equally split between sets on vines and branches less than

10 cm in diameter and those greater than 10 cm in diameter.

The reproductive state of the nine total specimens collected in the reserve was as follows: four scrotal adult males, two young males with abdominal testes, and three females with enlarged mammae (none lactating). The females possessed a mammary complement typical of *Eliurus* (1-0-2).

SPECIMENS EXAMINED—6.5 km SSW of Befingitra, 875 m (FMNH 154042; UA-SMG 6880); 9.2 km WSW of Befingitra, 1260 m (FMNH 154043, 154045, 154246, 154247, 154248; UA-SMG 6974, 6980).

Eliurus tanala Major, 1896b

DISTRIBUTION—Seven individuals of this handsome species, with its cream-colored venter and white caudal plume set against dark gray upperparts, were collected at 875 and 1260 m in the RS d'Anjanaharibe-Sud. As argued in Chapter 11, we tentatively assign these specimens to *Eliurus tanala* until the status and morphological limits of *E. ellermani* are evaluated.

ECOLOGY AND REPRODUCTION—Trapping results indicate that this species is largely terrestrial. Four of six individuals captured at 1260 m were taken in the same trap set placed on the ground. The ground was wet in the vicinity of the trap, set within 5 m of a stream and by an opening under a large boulder. A fifth individual was obtained a few meters away in another ground set this one under a clump of root material and next to the river. The only *Eliurus tanala* taken in an arboreal set was located in a tangle of vines and broken branches, 1 m above ground.

One evening, about 19:00 hr, a rodent was observed in the kitchen area of the 875 m camp, clambering over a makeshift table and feeding on rice. After a fumbled attempt was made to grab it, the animal awkwardly scrambled up the vertical trunk (15 cm diameter) of a *Pandanus* next to the table and remained motionless on the tree's bole until it was captured by hand. The animal, the lone example of *Eliurus tanala* obtained at 875 m, mounted the vertical trunk with considerable difficulty.

Four of seven specimens collected, three males and one female, were clearly young and reproductively immature. The other male was an adult with scrotal testes; the mammae (1-0-2) of two adult females were conspicuously large, but nei-

ther contained embryos or discernable placental scars.

SPECIMENS EXAMINED—6.5 km SSW of Befingitra, 875 m (FMNH 154049); 9.2 km WSW of Befingitra, 1260 m (FMNH 154050, 154051, 154249, 154250; UA-SMG 6977, 6979).

Eliurus webbi Ellerman, 1949

DISTRIBUTION—In the RS d'Anjanaharibe-Sud, *Eliurus webbi* was captured only in the 875 m zone. A parallel elevational distribution was found in the RNI d'Andringitra, where this species was trapped at 720 m and 810 m but not at higher elevations (Goodman & Carleton, 1996). Elsewhere in Madagascar, its distribution is predominantly lowland moist forest, although it has been recorded as high as 1525 m (Carleton & Schmidt, 1990; Carleton, 1994).

ECOLOGY AND REPRODUCTION—All four *Eliurus webbi* obtained in the standardized trap lines were trapped on limbs and vines, two each on those less than 10 cm in diameter and those greater than 10 cm in diameter. Another four individuals captured at 875 m were equally split between terrestrial and arboreal sets.

Evidence of ongoing reproduction was apparent among the eight *Eliurus webbi* collected. Two adult males possessed scrotal testes, and one adult female was lactating. Another three females had large mammae, and two of these each retained two placental scars. A younger male and female, presumably immature, showed no signs of reproduction. Mammae formulae varied from 1-0-2 (n = 4) to 1-0-1 (n = 1).

The high level of reproductive activity contrasts with the condition found in the sample of *Eliurus webbi* collected in November and December 1993 in the RNI d'Andringitra. There, only one of 16 males was a fully scrotal adult, and just two of seven females had enlarged mammae (Goodman & Carleton, 1996). Nor did any female dissected possess fetuses or placental scars. The great distance between the RS d'Anjanaharibe-Sud (14°45'S) and the RNI d'Andringitra (22°13'S), situated almost at the northern and southern extremes of Madagascar's eastern highlands, suggests geographic or seasonal variation in the breeding cycle of this species.

SPECIMENS EXAMINED—6.5 km SSW of Befingitra, 875 m (FMNH 154035, 154036, 154037, 154038, 154044, 154251, 154252; UA-SMG 6860).

Gymnuromys roberti Major, 1896c

DISTRIBUTION—Although known from relatively few sites, *Gymnuromys roberti* appears to be broadly distributed in humid forest found along the eastern versant of Madagascar. Based on specimens then available, Carleton and Schmidt (1990) noted its occurrence from the vicinity of Vondrozo (ca. 22°48'S) north to Périnet (or RS d'Analamazaotra, ca. 19°S). The documentation of *G. roberti* in the RS d'Anjanaharibe-Sud extends its known distribution 480 km to the north (ca. 14°45'S), still within the limits of the eastern humid forest domain.

Only three individuals of *Gymnuromys roberti* were trapped during the 1994 survey, all at 1260 m. In the RNI d'Andringitra, this species was similarly captured in small numbers but at all four elevational zones between 710 and 1625 m (Goodman & Carleton, 1996).

ECOLOGY AND REPRODUCTION—*Gymnuromys roberti* appears to be an exclusively terrestrial rat. One specimen was taken on the ground at the opening of a small hole leading under rocks and small roots, and the other two were captured in buckets, one in a pitfall line following bottomland along a river and the other in a line on a moderately sloping hillside. The buckets contained water from overnight rains, which probably hindered escape by jumping. Of the three individuals collected, two were adults, a male with testes partially descended and a female with slightly enlarged mammae (1-0-2), and the third was a juvenile female.

SPECIMENS EXAMINED—9.2 km WSW of Befingitra, 1260 m (FMNH 154056, 154057, 154268).

Nesomys rufus Peters, 1870

DISTRIBUTION—The presence of this comparatively large (Table 12-2), brightly colored rodent in the RS d'Anjanaharibe-Sud was expected based on previous records of its occurrence on the western and eastern slopes of the Tsaratanana Massif and its widespread distribution in eastern forest (Carleton & Schmidt, 1990). The species was captured in the higher zones of the RS d'Anjanaharibe-Sud (1260, 1550, and 1950 m), occupying a middle to upper montane belt like that documented on the Andringitra Massif (Goodman & Carleton, 1996).

ECOLOGY AND REPRODUCTION—As found in previous field studies, *Nesomys rufus* is wholly terrestrial and seems to prefer forest with an unclut-

tered understory and relatively thick mat of leaf litter (Ryan et al., 1993; Goodman & Carleton, 1996). Fourteen of 15 individuals were trapped in close proximity to tree roots and trunks, the 15th in a passageway under a shrubby thicket. In view of its preference for relatively open understory, this diurnal or crepuscular species could be seen moving about the forest floor, often in areas near large trees with partially exposed and extensive root systems, in which they locate their burrows. The species was usually observed to forage in the early morning and late afternoon, but on occasion it was active during the middle of the day.

The reproductive condition of the 15 *Nesomys rufus* varied but indicated active breeding. Six of eight males possessed fully scrotal testes with generally highly convoluted epididymides; the other two males had abdominal testes. Three of seven females were lactating, one with four fresh placental scars, but none with embryos in utero. The remaining females had small, inconspicuous mammae, and two of those, by their size, appeared to be recently weaned subadults. A high incidence of reproductive activity was also evident among the *N. rufus* captured in the RNI d'Andringitra during a survey undertaken in November and December 1993 (Goodman & Carleton, 1996).

SPECIMENS EXAMINED—9.2 km WSW of Befingitra, 1260 m (FMNH 154058–154061, 154269, 154270, 154274; UA-SMG 6996); 11 km WSW of Befingitra, 1550 m (FMNH 154062, 154063; UA-SMG 7028); 12.2 km WSW of Befingitra, 1950 m (FMNH 154271–154273; UA-SMG 7099).

Voalavo gymnocaudus Carleton and Goodman, 1998

DISTRIBUTION—During the 1994 inventory, three individuals of this small nesomyine (Table 12-2) were captured, all at 1950 m just below the summit. From 4 to 12 February 1996, Franco Andreone, Museo Regionale di Scienze Naturali, Torino, conducted a herpetological survey of the western slopes of the RS d'Anjanaharibe, between 1200 and 1600 m, and captured two more individuals of *Voalavo gymnocaudus* in pitfall buckets. The altitude of their collection is estimated to be 1300 m (Andreone, pers. comm.) and in a zone of montane forest distinctly drier than the 1950 m site. The flora in this section of the reserve is moist montane forest in primary condition. These additional records suggest that the species ranges across the montane/sclerophyllous forest zone of the Anjanaharibe-Sud Massif, from approximately 1300 m to 1950 m near the summit. Beyond these two localities and five specimens, the distribution of the newly discovered genus is unknown.

ECOLOGY AND REPRODUCTION—Of the specimens collected in 1994, two individuals were obtained on the ground, by the opening of a hole into the base of a large tree and under tree roots in a natural tunnel that appeared to be a distinctly trampled runway, and the third was obtained on a horizontal, deeply moss-covered limb (28 cm diameter with, and 21 cm diameter without, the moss) of a large tree. The second and third trap locations were within 5 m of one another. The habitat where *Voalavo gymnocaudus* were captured in 1994 is dwarf upper montane/sclerophyllous forest, a vegetational belt found just below the summit and typified by lush epiphytic growth and profuse moss cover on plant and ground surfaces (see Chapter 11). Although little rain fell during the brief visit in late November, the upper slopes around the 1950 m camp were often shrouded in clouds, and mossy surfaces were generally drenched with moisture.

Two of three individuals taken in 1994 are males, one adult with scrotal testes (7 × 5 mm) and distended, convoluted epididymides and one younger individual with undescended testes. The female had one placental scar on each uterine horn but no embryos and retained slightly enlarged mammae (1-0-2). The two individuals collected on the western slopes in February 1996 were an adult female, with distended mammae and apparently having nursed, and a young male, with testes abdominal in position.

SPECIMENS EXAMINED—12.2 km WSW of Befingitra, 1950 m (FMNH 154040, 154041, 154267); RS d'Anjanaharibe-Sud, western slope, 14°46′S, 49°26′E, ca. 1300 m (FMNH 156162, 156163).

Discussion

As a preamble to our discussion, we emphasize the preliminary nature of any attempt to formulate definitive statements about nesomyine diversity patterns, distributions, ecology, and reproductive biology. Little critically gathered information is available on this group, and much of that has emerged in just the past decade. Because the field study of the RS d'Anjanaharibe-Sud was conducted over a period of less than 2 months, the

window of time is too brief to support conclusions about reproductive seasonality and other populational phenomena or to rigorously contrast the findings with those from distant sites, such as the RNI d'Andringitra. Additional longer-term, site-intensive survey work is necessary to document whether clear patterns exist, particularly along altitudinal transects, and to understand their genesis. Finally, we stress that although important advances in our knowledge of the distribution and kinds of nesomyine rodents have been made in the past decade, there remain substantial geographic and taxonomic deficiencies that impede thorough comparisons of rodents from various places on the island (Carleton & Schmidt, 1990; see also Voss & Emmons, 1996, for a continental perspective on tropical diversity foundations). The additions of new genera and species to the Nesomyinae, through field discoveries and museum-based revisions (Carleton, 1994; Carleton & Goodman, 1996; Chapter 11), are revealing the unsuspected variety of an insular rodent group once described "as an exceptionally poor fauna with little speciation" (Paulian, 1984: p. 153).

Trapping Effort and Sampling Confidence

The 1994 small-mammal survey of the eastern slopes of the RS d'Anjanaharibe-Sud, from 875 in lowland moist forest, to 1260 and 1550 m in montane forest, and through 1950 m in sclerophyllous forest, produced nine species of native rodents as well as the ubiquitous *Rattus rattus*. Only two nesomyines were previously documented from the area (*Eliurus minor* and *Nesomys rufus*), and the inventory thus added records of an additional seven kinds, including a new species of *Eliurus* and a new genus and species of Nesomyinae (Chapter 11). During 7 weeks of field work, 2,600 trap-nights of sampling effort were apportioned among the four elevation sites (Table 12-1, Fig. 12-2) and yielded 117 mammals (Table 12-4), including 101 rodents, 15 insectivores (*Setifer setosus, Microgale cowani, M. dobsoni, M. gymnorhyncha, M. monticola, M. principula,* and *M. talazaci*; see Chapter 10), and one lemur (*Cheirogaleus major*; see Chapter 14).

Overall trap success, based on all small mammals captured (rodents, insectivores, and lemur) and total trap-nights (2,600), was highest at 1260 m (10.5%, 63 animals in 600 trap-nights) and ranged from 1.8 to 4.8% at the other three locales (875 m: 1.8%, 18 animals in 1,000 trap-nights;

1550 m: 4.8%, 24 animals in 500 trap-nights; and 1950 m: 2.4%, 12 animals in 500 trap-nights). When results are restricted to rodents obtained in the first 500 trap-nights within an elevational zone (the standardized trapping regimen), the percentage of trap return is nearly the same (Table 12-4), varying from 2.4% (at 875 and 1950 m) to 10.6% (1260 m). Except for the slightly higher success rate at 1260 m (>10%), these percentages are more or less typical of trap-line efficiencies from other rodent surveys at different elevational zones on Madagascar (Stephenson, 1993; Goodman & Ganzhorn, 1994; Stephenson et al., 1994; Goodman & Carleton, 1996; Goodman et al., 1996) and on other large Old World tropical islands (Heaney et al., 1989; Rickart et al., 1991, 1993).

Most rodent species captured in the RS d'Anjanaharibe-Sud may be generally characterized as either terrestrial or scansorial. Two species are strictly ground-dwelling (*Gymnuromys roberti* and *Nesomys rufus*), and one is probably strictly arboreal (*Brachytarsomys albicauda*), habits that are predicted by the bodily proportions and hind-foot morphology of the species. The activity sphere and locomotory mode of the remainder may be termed scansorial, although three were more often trapped on the ground (*Rattus rattus, Eliurus grandidieri,* and *E. tanala*) and three others in predominantly arboreal situations (*E. majori, E. minor,* and *E. webbi*). Too few *Voalavo gymnocaudus* were obtained to say much about its climbing behavior, but the animal's broad hind-feet and relatively long tail intimate scansorial proclivities. At other sites, such as RNI d'Andringitra, *E. webbi* is known to inhabit subterranean burrows, and although some individuals were trapped on the ground, the majority were obtained from arboreal sets (Goodman, 1994; Goodman & Carleton, 1996). No pronounced intraspecific trend was found in proportions of individuals taken on and off the ground; in contrast, there appeared to be shifts in microhabitat utilization by certain *Eliurus* species in zones of sympatry in the RNI d'Andringitra (Goodman & Carleton, 1996). Because no trap was placed more than 3 m off the ground (Table 12-1), canopy specialists, for which no evidence presently exists for such animals in Malagasy humid forest, would likely have been overlooked.

Two different types of evidence, derived from species accumulation curves and analogous results from other small-mammal inventories, support the premise that the trapping effort was suitable to establish basic rodent diversity within the
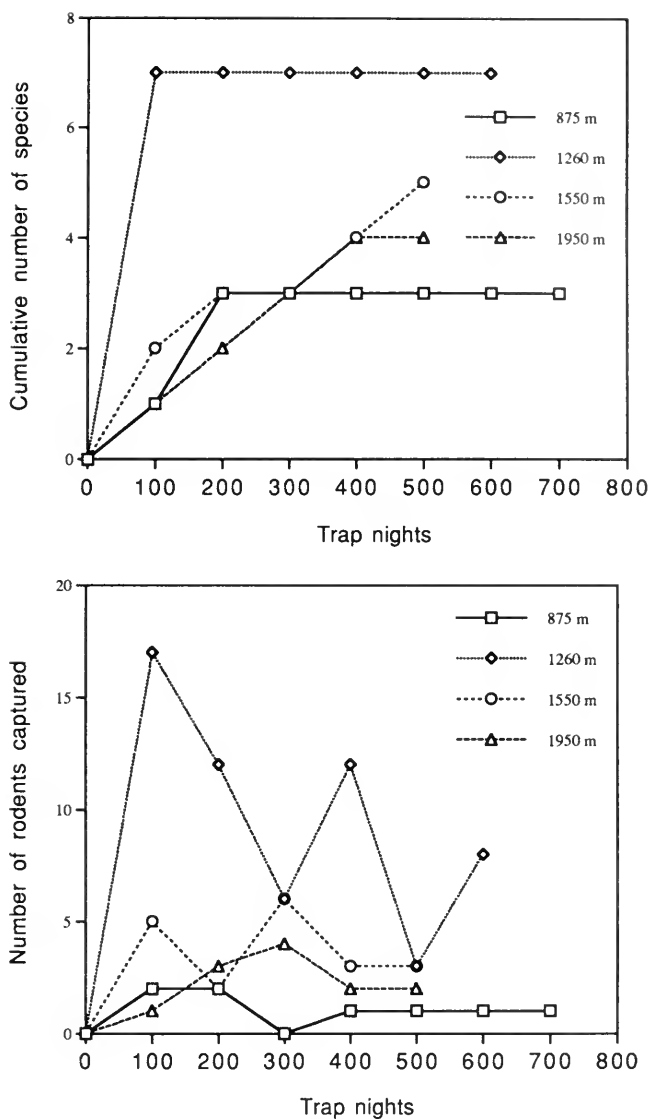
FIG. 12-2. Species accumulation curves (**top**) and trap success (**bottom**) of rodents plotted for each elevational zone against the number of trap-nights within the RS d'Anjanaharibe-Sud. Figures include both Nesomyinae and introduced *Rattus rattus*.

reserve. Plots of the cumulative number of species documented at each elevational zone over the duration of trapping disclose distinct plateaus before the end of each respective trapping session (Fig. 12-2). No additional rodent species were encountered after 100–400 trap-nights, depending on the elevational zone and the ultimate number of species eventually recorded at each. The asymptote in species accumulated per zone did not result from diminishing trap success, because there was

no parallel decrease in overall trap success during the course of the survey period (Fig. 12-2).

The number and composition of rodent species documented thus far for other places in the eastern humid forest provide circumstantial evidence about those that might be expected to occur in the RS d'Anjanaharibe-Sud. Three general localities, RNI d'Andringitra, Parc National de Ranomafana, and RS d'Analamazaotra (Périnet), qualify for such faunal comparisons: they are floristically

TABLE 12-4.   Number of individuals of small mammals captured in the RS d'Anjanaharibe-Sud during 500 trap-nights within the four elevational zones surveyed.

Species	875 m	1260 m	1550 m	1950 m
Microgale cowani			1	
Microgale dobsoni		2		
Microgale gymnorhyncha		1		
Microgale monticola			1	
Microgale principula			1	
Microgale talazaci		1	2	
Setifer setosus	4			
Rattus rattus	1	2	13	1
Eliurus grandidieri		21	1	
Eliurus majori		6	2	4
Eliurus minor	1	6		
Eliurus tanala		5		
Eliurus webbi	5			
Gymnuromys roberti		1		
Nesomys rufus		8	3	4
Voalavo gymnocaudus				3
Cheirogaleus major	1			
Total individuals	12	53	24	12
% Trap success	2.4	10.6	4.8	2.4
Total rodents	7	49	19	12
% Rodent trap success	1.4	9.8	3.8	2.4
Total nesomyine	6	47	6	11
% Nesomyine trap success	1.2	9.4	1.2	2.2

similar to the RS d'Anjanaharibe-Sud, encompass similar elevational spans, and have been extensively surveyed for rodents. Ten, eight, and nine species of Nesomyinae have been reported from Andringitra, Ranomafana, and Analamazaotra, respectively, whereas the native rodent fauna of the Anjanaharibe-Sud Massif totals nine (Table 12-5). The composition of rodents is broadly parallel among the four areas, largely due to several species (e.g., *Eliurus minor, E. tanala, E. webbi, Gymnuromys roberti,* and *Nesomys rufus*) that have extensive geographic ranges and broad elevational occurrence in eastern humid forests of the island. Five of the nine currently known species of *Eliurus* have been documented in the RS d'Anjanaharibe-Sud (Carleton, 1994; Chapter 11). On the basis of present distributional records, other nesomyine species reach their northern limits either in the region of the Sihanaka Forest (*Brachyuromys betsileoensis*) or the Central High Plateau (*B. ramirohitra, E. penicillatus, E. petteri,* and *Monticolomys koopmani*); none of these would be reasonably expected in the RS d'Anjanaharibe-Sud.

One other species may inhabit portions of the reserve, namely *Nesomys audeberti,* a form with an extensive north/south range in eastern lowland moist forest (Carleton & Schmidt, 1990; Goodman & Carleton, 1996). Because it has been collected in the vicinity of Antongil Bay and because the reserve contains some areas with lower-lying forest than the 875 m altitudinal zone, this large, white-bellied *Nesomys* may also occur locally. Excepting this species, we believe that the species accumulation curves and comparisons of species richness in eastern forest offer persuasive support that the rodent fauna of the RS d'Anjanaharibe-Sud has been largely, although perhaps not exhaustively, documented.

Elevation and Rodent Associations

No species of Nesomyinae was captured across the complete range of the altitudinal survey (875–1950 m), although two, *Eliurus majori* and *Nesomys rufus,* were found in the three higher zones (Table 12-6). As in the RNI d'Andringitra (Goodman & Carleton, 1996), the only clear example of elevational replacement of congeners involves *E. webbi* and *E. majori,* the former discovered only in the lowest zone (875 m) and the latter documented from 1260 to 1950 m. Two species in the Andringitra study, *E. minor* and *Gymnuromys*

TABLE 12-5. Comparison of nesomyine rodents documented to date for adequately censused regions in eastern humid forests.

Species	Anjanaharibe-Sud* 875–1950 m	Andringitra† 720–2450 m	Ranomafana‡ 575–1225 m	Analamazaotra§ 500–1300 m
Mus musculus		X		
Rattus rattus	X	X	X	X
Brachytarsomys albicauda	X		X	X
Brachyuromys betsileoensis		X	X	X
Brachyuromys ramirohitra		X		
Eliurus grandidieri	X			
Eliurus majori	X	X		
Eliurus minor	X	X	X	X
Eliurus petteri				X
Eliurus tanala	X	X	X	X
Eliurus webbi	X	X	X	X
Gymnuromys roberti	X	X	X	X
Monticolomys koopmani		X		
Nesomys audeberti		X	X	X
Nesomys rufus	X	X	X	X
Voalavo gymnocaudus	X			
Number of species of Nesomyinae	9	10	8	9

* This study.
÷ Goodman and Carleton (1996); Langrand and Goodman (1997); Goodman (unpubl. data).
‡ Carleton and Schmidt (1990); Ryan et al. (1993, in prep.); specimens in USNM.
§ Compiled from Carleton and Schmidt (1990); Carleton (1994); specimen in USNM; Stephenson (1993).

roberti, demonstrated seemingly broad ecological tolerance, occurring throughout the vegetational zones of the survey (720–1625 m) in relatively low densities (Goodman & Carleton, 1996). In contrast, their presence is apparently restricted in the RS d'Anjanaharibe-Sud (*E. minor* at the 875 and 1260 m levels and *G. roberti* only at 1260 m). We strongly suspect that their elevational range on this mountain is similarly extensive and that such differences are artifactual, arising through a combination of low density and chance and given the brevity of the trapping periods.

SPECIES RICHNESS—Nesomyine diversity was greatest at 1260 m, a survey zone with six species, but declined at both lower and higher elevations to four species (875 m) or three species (1550 and 1950 m) (Table 12-6). This midelevational peak in rodent species richness approximately coincides with the lower extent of montane forest, according to these trapping results. Furthermore, this elevational zone appears to be the region of the mountain where lowland and montane rodent faunas overlap, thus perhaps giving rise to a higher species richness at intermediate elevations. On

TABLE 12-6. Elevational zonation of rodents within the RS d'Anjanaharibe-Sud based on the trapping results of the 1994 inventory.

Species	875 m	1260 m	1550 m	1950 m
Rattus rattus	+	+	+	+
Brachytarsomys albicauda	+			
Eliurus grandidieri		+	+	
Eliurus majori		+	+	+
Eliurus minor	+	+		
Eliurus tanala	+	+		
Eliurus webbi	+			
Gymnuromys roberti		+		
Nesomys rufus		+	+	+
Voalavo gymnocaudus				+
Total species	5	7	4	4
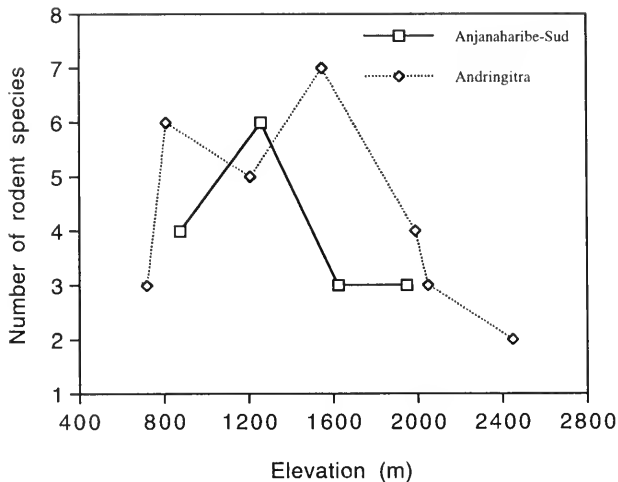
FIG. 12-3. Number of Nesomyinae rodents documented at various elevational zones in the humid forests of the RS d'Anjanaharibe-Sud (squares) and the RNI d'Andringitra (diamonds) using standardized trapping regimens. The Andringitra data are based on Goodman and Carleton (1996), Langrand and Goodman (1997), and Goodman (unpubl. data).

the Andringitra Massif, a site with typical vegetational zonation of eastern humid forest (Lewis et al., 1996), the highest species richness of native rodents, with seven species, was found at 1625 m (Fig. 12-3); at lower elevations species richness varied from three species at 720 m to six at 810 and 1210 m; at higher elevations it varied from five at 1990 m (just below tree line) to one at 2050 and 2450 m (Goodman & Carleton, 1996; Langrand & Goodman, 1997; Goodman, unpubl. data). The pattern at Andringitra and Anjanaharibe-Sud of rodent species richness along an elevational gradient appears to be more or less typical of other mountains in the Old World tropics and subtropics, including continental land masses and large islands, where the greatest rodent diversity is generally within the upper portion of montane forest (e.g., Rupp, 1980; Yalden, 1988; Heaney & Rickart, 1990; Yu, 1994). One of the better examples from Old World tropical forests of a midelevational bulge in rodent species richness is along the slopes of Mount Kinabalu, Borneo, where rodent diversity peaks at 1400 m across a transect from about 700 to 3200 m (Md. Nor, pers. comm.). This pattern of midelevational humps in species richness has been noted for many other groups of tropical invertebrates and vertebrates (Rosenzweig & Abramsky, 1993; Rahbek, 1995, 1997), but see Patterson et al. (in press) for a different pattern in the New World tropics.

RELATIVE POPULATION DENSITY AND BIOMASS—

As with species richness, relative density of rodent populations, as estimated by the number of individuals per 100 m of trap line, reached its highest level at 1260 m, with 9.3 individuals/100 m (Table 12-7). The highest density measured at any other elevation was about half this number (4.7 individuals/100 m at the 1550 m locality) and was smallest at the lowest elevation sampled, 875 m (1.0 individuals/100 m). Furthermore, the peak in estimated population density for each species of Nesomyinae was likewise recorded in the 1260 m zone; however, the variation in relative numbers of *Eliurus majori* and *Nesomys rufus,* found in three of four zones (1260–1950 m), is trivial across this 700 m swath of montane forest. Only the introduced *Rattus rattus* deviated from this pattern and, as measured by total number of captures or relative density, was most common in the 1550 m zone.

In the RNI d'Andringitra, sparse population densities were also reported for the lowest elevation sampled, 720 m in lowland moist forest, but density increased regularly with ascension into montane zones (Goodman & Carleton, 1996). Unlike Anjanaharibe-Sud, the greatest density was instead measured at the highest point of the transect, 1625 m within the lower reaches of sclerophyllous forest. For example, nearly a fourfold increase in the relative density of *Nesomys rufus* was recorded between 810 and 1625 m.

Because the nine species trapped in the RS d'Anjanaharibe-Sud vary 10-fold in average adult

Species	875 m (730)	1260 m (520)	1550 m (396)	1950 m (423)	Grand† mean
Rattus rattus	0.13	0.38	3.25	0.24	0.82
Eliurus grandidieri		3.99	0.25		2.40
Eliurus majori		1.14	0.50	0.96	0.90
Eliurus minor	0.13	1.14			0.56
Eliurus tanala		0.95			0.95
Eliurus webbi	0.69				0.69
Gymnuromys roberti		0.19			0.19
Nesomys rufus		1.52	0.75	0.96	1.05
Voalavo gymnocaudus				0.72	0.72
All rodents	0.96	9.31	4.75	2.88	4.20
% Captures of native rodents	86.5	95.9	31.6	91.7	80.5

* Number in parentheses is total length (in m) of trap lines for each zone.

† Averaged only for elevational zones in which a species was captured.

body weight (Table 12-2), ranging from around 22 g (*Voalovo gymnocaudus*) to more than 200 g (*Brachytarsomys albicauda*), rodent abundance on the slopes of the reserve may differ when measured by relative biomass compared with estimates of population density. However, the pattern of rodent biomass does parallel that derived for density estimates (Table 12-7), attaining the largest values at 1260 m whether viewed as total biomass or as average biomass per species (Table 12-8). The 1260 m bulge in relative biomass does not appear to be simply related to species diversity, because the zone also supports a higher average total biomass per species than do others on the massif. All measures of rodent abundance, species diversity, population density, and standing biomass, suggest that the habitat at 1260 m, near the lower boundary of montane forest, is the most productive within the RS d'Anjanaharibe-Sud.

Again, these results depart slightly from the picture derived for the rodent fauna of RNI d'Andringitra (Goodman & Carleton, 1996). There, estimated total biomass of rodents increased in relation to elevation, being highest at the top of the transect (1625 m), but the largest average biomass per species was recorded for a lower site (1210 m). Nevertheless, species diversity and most indices of abundance within the reserves appear to be closely coupled, with higher population densities and total biomass obtained in the zone having the most species (1625 m in the RNI d'Andringitra versus 1250 m in the RS d'Anjanaharibe-Sud). In view of the unknown level of sampling error inherent in these statistics and sample comparisons, further long-term investigations are required to verify whether the altitudinal profiles of species richness and population abundances are meaningfully different between

Species	875 m	1260 m	1550 m	1950 m
Rattus rattus	106	211	1,374	106
Eliurus grandidieri		1,109	53	
Eliurus majori		565	188	377
Eliurus minor	37	221		
Eliurus tanala		530		
Eliurus webbi	360			
Gymnuromys roberti		156		
Nesomys rufus		1,287	482	643
Voalavo gymnocaudus				66
Number of species	3	7	4	4
Total biomass	503	4,079	2,097	1,192
Average total biomass/species	168	583	524	298

* Summations from average weight of adults captured over the first 500 trap-nights within each zone.

TABLE 12-9. Multiple captures of rodents in a single trap within each elevational zone in the RS d'Anjanaharibe-Sud.*

Eleva-tion	Total species	Number of traps with captures	Traps with multiple captures	
			Same species	Different species
875 m	3	11	1	0
1260 m	6	35	12	8
1550 m	4	11	4	2
1950 m	4	9	2	0

* Not standardized for trap-nights.

the RS d'Anjanaharibe-Sud and RNI d'Andringitra.

Abundance and biomass have been used as measures of variation in species richness along elevational transects in the tropics (Terborgh, 1977; Graham, 1990). The relationship between specific diversity and these two factors seems to be consistent with the distribution of rodents on mountains in Madagascar. Further studies that collate aspects of forest productivity and its association with rodent species richness may help to sort out what forces mold these patterns. The possibility that the elevational distribution of rodents and their density vary between mountains on Madagascar could provide a natural system to explore hypotheses associated with productivity models (Rosenzweig & Abramsky, 1993).

MULTIPLE CAPTURES IN SINGLE TRAP SETS—In this section, instances of multiple captures by the same trap set are consolidated, both those involving individuals of the same species and those belonging to different species. We compile such examples, not necessarily as any indication of competition, but simply to document microhabitat overlap and local syntopy. Long-term, single-site field studies are required to conclude partitioning of resources or interference competition for them and to demonstrate social organization and mating systems.

At least one trap station within each elevational zone secured two or more conspecifics, but the number of such multiple successes varied considerably. The only discernable pattern is the predictable correlation that the level with the most rodent species and largest populations, 1260 m, contained the most instances of multiple captures (Table 12-9). In a few cases, three or more individuals of *Rattus rattus, Eliurus grandidieri,* and *E. tanala* were taken in the same trap in various

combinations over the term the line was in place, suggesting some sort of "trap competition" (Patterson et al., 1989; Yu, 1994). The number of multiple captures in traps placed within this elevation zone deviated from a Poisson distribution ($p < 0.01$). No clear sex ratio pattern emerged for conspecifics taken in the same set, disallowing any inference about a species' social organization. Eight of 13 *R. rattus* captured at 1550 m were taken in three traps, all within 70 m of one another and on a man-made trail that had been in existence for several years. The age or sex of the trapped individuals supplies no evidence that these rodents were clearly living in family groups or monogamous couples. Rather, it appears that they have a clumped distribution along the trail in this elevational zone.

Like conspecific associations, the incidence of interspecific captures was highest at 1260 m (Table 12-9). All of these were taken in ground placements, although 43 of the 100 live traps in this zone were situated in arboreal settings. Examples of microhabitat overlap between species include the following: *Eliurus grandidieri* and *E. tanala,* in traps set under roots or boulders and within 5 m of a stream margin; *E. grandidieri* and *Rattus,* at an opening under roots and a small boulder; *E. grandidieri* and *Nesomys rufus,* in traps positioned at an opening in root entanglement and at the hollowed-out base of a massive tree; *E. grandidieri* and *E. majori,* in leaf litter close to a small stream; and *E. majori* and *Rattus,* at the opening of a large cavity under tree roots. In one case, on consecutive days, an *E. minor* and *Microgale gymnorhyncha* (FMNH 154028) entered a trap placed near an opening under roots and at the edge of dense herbaceous vegetation. The single above-ground trap station (at 1550 m) that yielded an interspecific catch involved *E. majori* and *Rattus,* collected in a trap placed 1.5 m high on a nearly horizontal tree trunk.

INTRA- AND INTERSPECIFIC DIFFERENCES IN REPRODUCTION—Knowledge of reproductive physiology and seasonality of breeding is meager for most species of Nesomyinae. Other than anecdotal observations, the only information published on variation along an elevational transect comes from the RNI d'Andringitra (Goodman & Carleton, 1996). Here we augment this previous study and summarize information on breeding condition of the Anjanaharibe-Sud rodents.

Levels of rodent reproduction were moderately high on the slopes of the RS d'Anjanaharibe-Sud, signs of active breeding evident in 55% (1950 m)

TABLE 12-10. Reproductive condition of all rodents captured (standard live traps and pitfall traps) in the RS d'Anjanaharibe-Sud.*

Species	875 m		1260 m		1550 m		1950 m		875–1950 m	
	A/S	M/F	A/S	M/F	A/S	M/F	A/S	M/F	A/S	M/F
Rattus rattus	0/1	0/1	4/0	4/0	7/1	4/4	0/1	1/0	11/3	9/5
Brachytarsomys albicauda	1/0	0/1							1/0	0/1
Eliurus grandidieri			13/13	10/16	1/0	0/1			14/13	10/17
Eliurus majori			4/4	7/1	2/0	2/0	2/2	0/4	8/6	9/5
Eliurus minor	1/1	1/1	5/2	5/2					6/3	6/3
Eliurus tanala	0/1	1/0	3/3	3/3					3/4	4/3
Eliurus webbi	6/2	3/5							6/2	3/5
Gymnuromys roberti			2/1	1/2					2/1	1/2
Nesomys rufus			5/3	6/2	2/2	1/3	2/1	1/2	9/6	8/7
Voalavo gymnocaudus							2/1	2/1	2/1	2/1
Total	8/5	5/8	36/26	36/26	12/3	7/8	6/5	4/7		
% Individuals captured in reproductive state	62		58		80		55			

* A = adults; F = females with large mammae, carry embryos, or lactating; M = males with scrotal testes; and S = subadults.

to 80% (1550 m) of the specimens collected within an elevation (Table 12-10). Moreover, no clinal trend with elevation is suggested for this data. In the RNI d'Andringitra, there was a directional pattern of increasing reproductive activity at higher altitudes, ranging from only 25% of the rodents sampled at 720 m to more than 80% at 1625 m. Whether such a trend is manifested within any species in the RS d'Anjanaharibe-Sud is unclear, because few taxa were found across a broad range of altitudes or the number of individuals captured is insufficient to draw conclusions.

The timing of the Anjanaharibe survey (mid-October through November) was chronologically in advance of the one conducted in Andringitra (mid-November through mid-December). In the survey of the RNI d'Andringitra (22°13′S), very few juvenile or subadult rodents were captured. Furthermore, the ratio of adults to subadults and the number of adults in or approaching a sexually mature state indicate that the Andringitra inventory was conducted at the beginning of a reproductive season. In the RS d'Anjanaharibe-Sud (14°45′S), the proportions are different, particularly for the genus *Eliurus,* in which a smaller percentage of the individuals trapped were in reproductive condition and a significant portion were subadults. Such differences in the reproductive condition and age structure of rodents captured at these two sites may implicate seasonal or latitudinal factors to account for the considerable variation in these variables.

Acknowledgments

Literature Cited

Barden, T. L., M. I. Evans, C. J. Raxworthy, J.-C. Razafimahaimodison, and A. Wilson. 1991. The mammals of Ambatovaky Special Reserve, pp. 5-1–

5-20. *In* Thompson, P. M., and M. I. Evans, eds., A Survey of Ambatovaky Special Reserve, Madagascar. Madagascar Environmental Research Group, London.

CARLETON, M. D. 1994. Systematic studies of Madagascar's endemic rodents (Muroidea: Nesomyinae): Revision of the genus *Eliurus*. American Museum Novitates, **3087:** 1–55.

CARLETON, M. D., AND S. M. GOODMAN. 1996. Systematic studies of Madagascar's endemic rodents (Muroidea: Nesomyinae): A new genus and species from the Central Highlands, pp. 231–256. *In* Goodman, S. M., ed., A floral and faunal inventory of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: With reference to elevational variation. Fieldiana: Zoology, **85:** 1–319.

CARLETON, M. D., AND G. G. MUSSER. 1984. Muroid rodents, pp. 289–379. *In* Anderson, S., and J. K. Jones, Jr., eds., Orders and Families of Recent Mammals of the World. John Wiley and Sons, New York, 686 pp.

CARLETON, M. D., AND D. F. SCHMIDT. 1990. Systematic studies of Madagascar's endemic rodents (Muroidea: Nesomyinae): An annotated gazetteer of collecting localities of known forms. American Museum Novitates, **2987:** 1–36.

DUBOIS, J.-Y., D. RAKOTONDRAVONY, C. HÄNNI, P. SOURROUILLE, AND F. F. CATZEFLIS. 1996. Molecular evolutionary relationships of three genera of Nesomyinae, endemic rodent taxa from Madagascar. Journal of Mammalian Evolution, **3:** 239–260.

DUCKWORTH, J. W., AND F. RAKOTONDRAPARANY. 1990. The mammals of Marojejy, pp. 54–60. *In* Safford, R., and Duckworth, J. W., eds., A Wildlife Survey of the Marojejy Nature Reserve, Madagascar. International Council for Bird Preservation, Cambridge, 172 pp.

ELLERMAN, J. R. 1949. The Families and Genera of Living Rodents. Volume 3, Appendix II [Notes on the rodents from Madagascar in the British Museum, and on a collection from the island obtained by Mr. C. S. Webb]. British Museum (Natural History), London, v + 210 pp.

GOODMAN, S. M. 1994. A description of the ground burrow of *Eliurus webbi* (Nesomyinae) and a case of cohabitation with an endemic bird (Brachypteraciidae, *Brachypteracias*). Mammalia **58:** 670–672.

———. 1995. *Rattus* on Madagascar and the dilemma of protecting the endemic rodent fauna. Conservation Biology, **9:** 450–453.

GOODMAN, S. M., A. ANDRIANARIMISA, L. E. OLSON, AND V. SOARIMALALA. 1996. Patterns of elevational distribution of birds and small mammals in the humid forest of Montagne d'Ambre Madagascar. Ecotropica, **2:** 87–98.

GOODMAN, S. M., AND M. D. CARLETON. 1996. The rodents of the Réserve Naturelle Intégrale d'Andringitra, Madagascar, pp. 257–283. *In* Goodman, S. M., ed., A floral and faunal inventory of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: With reference to elevational variation. Fieldiana: Zoology, **85:** 1–319.

GOODMAN, S. M., AND J. GANZHORN. 1994. Les petits mammifères, pp. 58–63. *In* Goodman, S. M., and O. Langrand, eds., Inventaire biologique Forêt de Zombitse. Recherches pour le Développement, Série Sciences biologiques, No. Spécial. Centre d'Information et de Documentation Scientifique et Technique, Antananarivo, 106 pp.

GOODMAN, S. M., J. GANZHORN, L. E. OLSON, M. PIDGEON, AND V. SOARIMALALA. In press. Annual variation in species diversity and relative density of rodents and insectivores in the Montagne d'Ambre National Park, Madagascar. Ecotropica.

GOODMAN, S. M., AND D. RAKOTONDRAVONY. 1996. The Holocene distribution of *Hypogeomys* (Rodentia: Muridae: Nesomyinae) on Madagascar, pp. 283–293. *In* Lourenço, W. R., ed., Biogéographie de Madagascar. Editions ORSTOM, Paris, 588 pp.

GRAHAM, G. L. 1990. Bats vs. birds: Comparisons among Peruvian volant vertebrate faunas along an elevational gradient. Journal of Biogeography, **17:** 657–668.

HEANEY, L. R., P. D. HEIDEMAN, E. A. RICKART, R. B. UTZURRUM, AND J. S. H. KLOMPEN. 1989. Elevational zonation of mammals in the central Philippines. Journal of Tropical Ecology, **5:** 259–280.

HEANEY, L. R., AND E. A. RICKART. 1990. Correlations of clades and clines: Geographic, elevational, and phylogenetic distribution patterns among Philippine mammals, pp. 321–332. *In* Peters, G., and R. Hutterer, eds., Vertebrates in the Tropics. Museum Alexander Koenig, Bonn, 585 pp.

JENKINS, P. D. 1987. Catalogue of primates in the British Museum (Natural History) and elsewhere in the British Isles. Part IV. Suborder Strepsirrhini, including the subfossil Madagascan lemurs and Family Tarsiidae. British Museum (Natural History), London, x + 189 pp.

LANGRAND, O. AND S. M. GOODMAN. 1997. Inventaire des oiseaux et des micro-mammifères des zones sommitales de la Réserve Naturelle Intégrale d'Andringitra. Akon'ny Ala, **20:** 39–54.

LEWIS, B. A., P. B. PHILLIPSON, M. ANDRIANARISATA, G. RAHAJASOA, P. J. RAKOTOMALAZA, M. RANDRIAMBOLOLONA, AND J. F. MCDONAGH. 1996. A study of the botanical structure, composition, and diversity of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar, pp. 24–75. *In* Goodman, S. M., ed., A floral and faunal inventory of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: With reference to elevational variation. Fieldiana: Zoology, **85:** 1–319.

MAJOR, C. I. FORSYTH. 1896a. On the general results of a zoological expedition to Madagascar in 1894–96. Proceedings of the Zoological Society of London, **1896:** 971–981.

———. 1896b. Descriptions of four additional new mammals from Madagascar. Annals and Magazine of Natural History, series 6, **18:** 461–463.

———. 1896c. Diagnoses of new mammals from Madagascar. Annals and Magazine of Natural History, series 6, **18:** 318–325.

MUSSER, G. G. 1987. The mammals of Sulawesi, pp. 73–93. *In* Whitmore, T. C., ed., Biogeographical Evolution of the Malay Archipelago. Clarendon Press, Oxford.

MUSSER, G. G., AND M. D. CARLETON. 1993. Family

Muridae, pp. 501–755. *In* Wilson, D. E., and D. M. Reeder, eds., Mammal Species of the World: A Taxonomic and Geographic Reference, 2nd ed. Smithsonian Institution Press, Washington, D.C., 1,026 pp.

NICOLL, M. E., AND O. LANGRAND. 1989. Madagascar: Revue de la conservation et des Aires Protégées. World Wide Fund for Nature, Gland, Switzerland, xvii + 374 pp.

NICOLL, M. E., F. RAKOTONDRAPARANY, AND V. RANDRIANASOLO. 1988. Diversité des petits mammifères en forêt tropicale humide de Madagascar, analyse préliminaire, pp. 241–252. *In* Rakotovao, L., V. Barre, and J. Sayer, eds., L'Equilibre des ecosystèmes forestiers à Madagascar: Actes d'un séminaire international. International Union for the Conservation of Nature and Natural Resources, Gland, Switzerland, 338 pp.

PATTERSON, B. D., P. L. MESERVE, AND B. K. LANG. 1989. Distribution and abundance of small mammals along an elevational transect in temperate rainforests of Chile. Journal of Mammalogy, **70:** 67–78.

PATTERSON, B. D., D. F. STOTZ, S. SOLARI, J. W. FITZPATRICK, AND V. PACHECO. In press. Contrasting patterns of elevational zonation for birds and mammals in the Andes of southeastern Peru. Journal of Biogeography.

PAULIAN, R. 1984. Introduction to the mammals, pp. 151–154. *In* Jolly, A., P. Oberlé, and R. Albignac, eds., Key Environments: Madagascar. Pergamon Press, Oxford, xviii + 239 pp.

PETERS, W. 1870. Uber *Nesomys rufus,* eine neue gattung und art madagascarischer nager. Sitzungs-Berichte der Gesellschaft naturforsender Freunde, Berlin, **1870:** 54–55.

PETTER, F. 1972. The rodents of Madagascar: The seven genera of Malagasy rodents, pp. 661–665. *In* Battistini, R., and G. Richard-Vinard, eds., Biogeography and Ecology in Madagascar. W. Junk B.V., The Hague, xv + 765 pp.

———. 1990. Relations de parenté des rongeurs de Madagascar. Atti dei Convegni Lincei, **85:** 829–837.

RADIMILAHY, C. 1997. Mahilaka, an eleventh to fourteenth-century Islamic port: The first impact of urbanism on Madagascar, pp. 342–377. *In* S. M. Goodman and B. D. Patterson, eds., Natural Change and Human Impact in Madagascar. Smithsonian Institution Press, Washington D.C., 432 pp.

RAHBEK, C. 1995. The elevational gradient of species richness: A uniform pattern? Ecogeography, **18:** 200–205.

———. 1997. The relationship among area, elevation, and regional species richness in Neotropical birds. The American Naturalist, **149:** 875–902.

RAKOTOZAFY, L. M. A. 1996. Étude de la constitution du régime alimentaire des habitants du site de Mahilaka du XIè au XIVè siècle à partir des produits de fouilles archéologiques. Doctorat de Troisième Cycle, Université d'Antananarivo.

RAND, A. L. 1932. Mission Franco-Anglo-Américaine à Madagascar: Notes de voyage. Oiseau et Revue Française d'Ornithologie, **2:** 227–282.

———. 1936. The distribution and habits of Madagascar birds: A summary of the field notes of the Mission Zoologique Franco-Anglo-Américaine à Madagascar. Bulletin of the American Museum of Natural History, **72:** 143–499.

RICKART, E. A., L. R. HEANEY, AND R. C. B. UTZURRUM. 1991. Distribution and ecology of small mammals along an elevational transect in southeastern Luzon, Philippines. Journal of Mammalogy, **72:** 458–469.

RICKART, E. A., L. R. HEANEY, P. D. HEIDEMAN, AND R. C. B. UTZURRUM. 1993. The distribution and ecology of mammals on Leyte, Biliran, and Maripipi Islands, Philippines. Fieldiana: Zoology, n.s., **72:** 1–62.

ROSENZWEIG, M. L., AND Z. ABRAMSKY. 1993. How are diversity and productivity related? pp. 52–65. *In* Ricklefs, R. E., and D. Schluter, eds., Species Diversity in Ecological Communities. University of Chicago Press, Chicago, 414 pp.

RUPP, H. 1980. Beiträge zur Systematik, Verbreitung und Ökologie äthiopischer Ergebnisse mehrerer Forschungsreisen. Saugetierkundliche Mitteilungen, **28:** 81–123.

RYAN, J. M., G. K. CREIGHTON, AND L. H. EMMONS. 1993. Activity patterns of two species of *Nesomys* (Muridae: Nesomyinae) in a Madagascar rain forest. Journal of Tropical Ecology, **9:** 101–107.

STEPHENSON, P. J. 1993. The small mammal fauna of Réserve Spéciale d'Analamazaotra, Madagascar: The effects of human disturbance on endemic species diversity. Biodiversity and Conservation, **2:** 603–615.

STEPHENSON, P. J., H. RANDRIAMAHAZO, N. RAKOTOARISON, AND P. A. RACEY. 1994. Conservation of mammalian species diversity in Ambohitantely Special Reserve, Madagascar. Biological Conservation, **69:** 213–218.

TERBORGH, J. 1977. Bird species diversity on an Andean elevational gradient. Ecology, **58:** 1007–1019.

THOMAS, O. 1895. On a new species of *Eliurus.* Annals and Magazine of Natural History, series 6, **16:** 164–165.

VOSS, R. S., AND L. H. EMMONS. 1996. Mammalian diversity in Neotropical lowland rainforests: A preliminary assessment. Bulletin of the American Museum of Natural History, **230:** 1–115.

WEBB, C. S. 1954. The odyssey of an animal collector. Longmans, Green, and Co., London, xv + 368 pp.

YALDEN, D. W. 1988. Small mammals of the Bale Mountains, Ethiopia. African Journal of Ecology, **26:** 281–294.

YU, H.-T. 1994. Distribution and abundance of small mammals along a subtropical elevational gradient in central Taiwan. Journal of Zoology, **234:** 577–600.

Chapter 13

Notes on the Bats of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar

Steven M. Goodman[1]

Abstract

Three bat species were collected in the Réserve Spéciale d'Anjanaharibe-Sud at 650 m: *Rousettus madagascariensis*, *Myotis goudoti*, and *Miniopterus fraterculus*. These species are broadly distributed across the island in both forested and disturbed areas.

Résumé

Trois espèces de chauve-souris ont été collectées dans la Réserve Spéciale d'Anjanaharibe-Sud à 650 m d'altitude: *Rousettus madagascariensis*, *Myotis goudoti*, et *Miniopterus fraterculus*. Ces espèces présentent une large distribution à travers toute l'île au sein de zones boisées et dégradées.

Introduction

In a recent monograph, Peterson et al. (1995) filled a long-standing void in information on Madagascar bats by summarizing distributional information and providing taxonomic revisions. Previously, the useful but out-of-date works on the island's Chiroptera were by Dorst (1947a,b, 1948). Even though Peterson et al. (1995) is based on original field work and a review of previous collections in museums, remarkably few areas of the island have been worked for bats.

Our knowledge of the bat faunas of most reserves is rudimentary or nonexistent (Nicoll and Langrand, 1989). One major exception is the Réserve Naturelle Intégrale (RNI) de Marojejy, just across the Andapa basin from the Réserve Speciale (RS) d'Anjanaharibe-Sud, where in 1989 a group from Aberdeen University conducted a survey of bats (Pont and Armstrong, 1990). Although only a few bats were captured in the RS

d'Anjanaharibe-Sud, this information complements that for the RNI de Marojejy and is presented herein.

Methods

In the village of Ranomafana (650 m elevation), along the Marolakana River and at the edge of the RS d'Anjanaharibe-Sud, three 12 m long × 2.6 m high nets were erected late one afternoon and left in place overnight. The nets were attended from dusk to 20:00 hr and checked several times during the night. The site was in a cleared area along the forest edge. Two nets spanned the river, and one net was at the ecotone between a banana plantation, the river margin, and secondary forest. In each of the four elevational zones (975, 1260, 1550, and 1950 m), nine nets were in operation for 5 days and nights to capture birds (see Chapter 8). No bats were captured in the bird nets.

Netted bats were prepared as specimens, which

[1] Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, IL 60605-2496 U.S.A.

are deposited in the Field Museum of Natural History, Chicago, and the Département de Biologie Animale, Université d'Antananarivo. Most of the bats were prepared as fluid-preserved specimens, and information is not available on internal reproductive organs or skulls for measurements.

Measurements

Measurements were made of animals in the flesh and of prepared crania. The abbreviations and definitions for measurements (all in mm except WT, which is in g) are as follows:

BBC = breadth of braincase, measured across the hamular processes of the squamosal at the point where they border the mastoid bullae

CM = canine–molar length, measured from the anterior alveolar border of a canine to posterior alveolar border of last molar

EL = ear length, measured from the base of the ear to the distalmost edge of the pinna

FA = forearm length, measured from the outside edge of the wrist to the outside edge of the elbow (with wing folded)

HF = hindfoot length, measured from the back edge of the heel to the end of the longest toe (not including claw)

IOB = interorbital breadth, the minimum distance across the frontal bones between the orbits (in Megachiroptera this was taken in front of the postorbital processes, and in Microchiroptera behind the postorbital processes)

ML = mandible length, measured from the midpoint of mandibular condyle to the anteriormost point of dentary

ONL = occipitonasal length, distance between the tip of the nasals and the posteriormost edge of the occiput, just above foramen magnum

TL = tail length, measured from the base of the tail (at right angles to the body) to the end of the distalmost vertebra

TOTL = total length of body and tail, measured from the nose tip to the end of the distalmost tail vertebra

TR = tragus length, measured from the base of tragus to the distalmost tip

WC = width across canines, measured across

the exterior-most alveolar base of the upper canines

WT = weight, measured in grams with Pesola spring scales. Animals weighing up to 10 g weighed to the nearest 0.1 g, and those weighing between 11 and 100 g were weighed to within 0.5 g

ZB = zygomatic breadth, greatest distance between the lateral surfaces of the zygomatic arches

Species Accounts

Family Pteropodidae

Rousettus madagascariensis Grandidier, 1929

Six *Rousettus madagascariensis* were captured at Ranomafana in the ecotone net. This species generally occurs in lowland areas, and the highest recorded altitude is 990 m (Bergmans, 1994). Measurements of the RS d'Anjanaharibe-Sud material (Table 13-1) fall within the ranges given by Bergmans (1994) and Peterson et al. (1995) for this species. *Rousettus madagascariensis* was the most commonly netted bat in the RNI de Marojejy, and all were taken in areas outside of primary forest and near agricultural areas (Pont and Armstrong, 1990).

REPRODUCTION—The six individuals consisted of two adult males with slightly scrotal testes, one subadult male with abdominal testes, one adult female with large teats and a perforated vagina, and two subadult females, both with small teats and imperforated vaginas.

Family Vespertilionidae

Myotis goudoti (A. Smith, 1834)

A single *Myotis goudoti* was captured in the ecotone net. Measurements of the individual are presented in Table 13-1. During the RNI de Marojejy survey, three *M. goudoti* were netted, two in a clearing in secondary forest and one outside the forest at a river margin (Pont and Armstrong, 1990).

REPRODUCTION—The specimen is a female with large mammae and a perforated vagina.

Table 13-1. Selected measurements of bats collected during the survey.

A External Measurements*

Species	Age	TOTL	TL	HF	EL	TR	FA	WT
Rousettus madagascariensis	Adult (n = 3)	131.3 ± 3.5 128–135	13.7 ± 0.6 13–14	15.6 ± 0.6 15–16	18.3 ± 1.2 17–19		70.7 ± 2.9 69–74	53.3 ± 5.4 49.5–59.5
	Subadult (n = 3)	127.0 ± 6.6 120–133	16.3 ± 3.1 13–19	15.7 ± 1.5 14–17	17.3 ± 0.6 17–18		69.7 ± 4.9 64–73	46.2 ± 10.1 35.5–55.5
Myotis goudoti	Adult	97	43	6	15	8	41	6.9
Miniopterus fraterculus	Adult	100	41	6	12	7	41	7.7

B Cranial Measurements

Species	Age	ONL	ZB	BBC	IOB	WC	CM³	ML
Rousettus madagascariensis	Subadult	32.3, 35.5	18.0, 20.2	13.5, 14.0	5.8, 6.4	6.1, 6.6	12.5, 12.7	25.6, 27.8
Myotis goudoti	Adult	14.5	9.5	7.8	3.1	4.1	5.7	11.1
Miniopterus fraterculus	Adult	14.9	7.8	8.1	3.3	4.1	5.9	10.5

* Descriptive statistics are presented as the mean ± SD, observed range, and number of specimens.

Miniopterus fraterculus Thomas and Schwann, 1906

The only individual of *Miniopterus* captured in the reserve was in one of the nets transversing the Marolakana River. On the basis of external (forearm length) and cranial measurements (Table 13-1), this individual is referred to *M. fraterculus* (Hill, 1993; Peterson et al., 1995). Members of this genus are exceptionally difficult to identify with external measurements. Pont and Armstrong (1990) netted five *Miniopterus* in the RNI de Marojejy in areas of secondary forest and outside the forest near a river margin. No specimens were collected, but on the basis of external measurements, at least two species of *Miniopterus* occur in that reserve.

REPRODUCTION—The single specimen is a female with small teats and an imperforated vagina.

Summary

Three bat species were recorded in the RS d'Anjanaharibe-Sud. All of these species have broad geographic ranges across Madagascar (Peterson et al., 1995) and occur in both humid and dry regions of the island. Our inventory of the bat fauna of the reserve was by no means exhaustive, and other species reported from the nearby RNI de Marojejy (Pont and Armstrong, 1990), including *Myzopoda aurita*, *Hipposideros commersoni*, and *Scotophilus robustus*, should presumably also occur in Anjanaharibe-Sud. Furthermore, *Pteropus rufus* has been previously reported from the reserve (Nicoll and Langrand, 1989).

Acknowledgments

Literature Cited

BERGMANS, W. 1994. Taxonomy and biogeography of African fruit bats (Mammalia, Megachiroptera). 4. The genus *Rousettus* Gray, 1821. Beaufortia, **44**: 79–126.

DORST, J. 1947a. Les chauves-souris de la faune Malgache. Bulletin du Muséum National d'Histoire Naturelle, séries 2, **19**: 306–313.

———. 1947b. Essai d'une clef de détermination des

chauve-souris Malgaches. Mémoires de l'Institut Scientifique de Madagascar, séries A, **1:** 81–88.

———. 1948. Biogéographie des Chiroptères malgaches. Mémoires de l'Institut Scientifique de Madagascar, séries A, **1:** 193–198.

HILL, J. E. 1993. Long-fingered bats of the genus *Miniopterus* (Chiroptera: Vespertilionidae) from Madagascar. Mammalia, **57:** 401–405.

NICOLL, M. E., AND O. LANGRAND. 1989. Madagascar: Revue de la conservation et des aires protégées. World Wide Fund for Nature, Gland, xvii + 374 pp.

PETERSON, R. L., J. L. EGER, AND L. MITCHELL. 1995. Chiroptères, vol. 84. Faune de Madagascar. Muséum National de Histoire Naturelle, Paris, 204 pp.

PONT, S. M., AND J. D. ARMSTRONG. 1990. A study of the bat fauna of the Réserve Naturelle Intégrale de Marojejy in north-east Madagascar: Report of the Aberdeen University expedition to Madagascar 1989. Department of Zoology, University of Aberdeen, Aberdeen, 57 pp.

Chapter 14

Lemurs of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar

Jutta Schmid[1] and Rachel Smolker[2]

Abstract

A survey was conducted between 16 October and 5 December 1994 in the Réserve Spéciale d'Anjanaharibe-Sud, a 32,100 ha area of humid forest in northeastern Madagascar. Study sites were centered at 865, 1260, 1550, and 1950 m altitude, and transects within each zone included a swath ±75 m altitude. In each elevational zone, the presence and abundance of lemur species were estimated using line transect methods. Eleven lemur species were recorded in the reserve. Population density decreased as elevation increased. Species richness was not affected by changes in elevation for the three lower transect zones, but only one species was recorded in the 1950 m zone. Important taxa found include *Allocebus trichotis* and *Daubentonia madagascariensis,* the presence of the latter inferred from traces of its distinctive feeding methods.

Résumé

Un inventaire des primates de la Réserve Spéciale d'Anjanaharibe-Sud, qui couvre 32.100 ha au nord-est de Madagascar, a été conduit du 16 Octobre au 5 Décembre 1994. Les sites d'étude étaient localises à 865, 1260, 1550, et 1950 m d'altitude et les transects réalisés au sein de chaque site avec un variation altitudinale de plus ou moins 75 m. Au sein de chaque site d'étude, la présence et l'abondance des espèces de lémuriens ont été estimées en utilisant la méthode de transect. Onze espèces de lémuriens ont été répertoriées dans la réserve. La densité des populations décroît en fonction de l'augmentation de l'altitude. La richesse spécifique ne présentait pas de variation en fonction de l'altitude au niveau des trois sites les plus bas, mais seulement une espèce a été répertoriée à 1950 m d'altitude. Les taxons remarquables qui ont été rencontrés comprennent *Allocebus trichotis* et *Daubentonia madagascariensis*. La présence de cette dernière espèce a été constatée à partir de traces caractéristiques qu'elle laisse dans sa quête et la consommation de nourriture.

Introduction

Madagascar contains an astounding level of endemic primate diversity and more endangered and

vulnerable primates than any other country in the world (Bourliere, 1985; Harcourt & Thornback, 1990; Mittermeier et al., 1994). Malagasy lemurs occupy a wide range of forests and vegetation types, including eastern humid forests, western dry forests, and spiny forest of the south. However, much of the forest throughout these regions has been replaced by a mosaic of cultivation and secondary formations, and the Central Plateau is almost totally deforested. The conservation of

---

[1] Deutsches Primatenzentrum, Kellnerweg 4, 37077 Göttingen, Germany, and Abteilung für Verhaltenphysiologie, Beim Kupferhammer 8, 72070 Tübingen, Germany.
[2] Museum of Zoology, University of Michigan, Ann Arbor, MI 48109, U.S.A.

Madagascar's rich and unique biota depends on the continued presence of forests.

The Réserve Spéciale (RS) d'Anjanaharibe-Sud covers 32,100 ha in eastern Madagascar with an elevational range from 500 to 2064 m, including primary and secondary lowland rainforest as well as moist montane forest (see Chapter 2). Little is known about the primates of this reserve, although Nicoll and Langrand (1989) reported seven lemur species. More adequately surveyed areas near the RS d'Anjanaharibe-Sud include the Réserve Naturelle Intégrale (RNI) de Marojejy (to the northeast) and Masoala Penisula (to the southeast). The survey reported here provides additional information on the distribution and abundance of lemur species for this part of Madagascar. Some information on habitat preferences and effects of habitat disturbance is also provided and may contribute toward more effective management of the RS d'Anjanaharibe-Sud forests.

Methods

Study Sites

Survey sites were at four different elevations along the eastern slope of the Anjanaharibe-Sud Massif. At the two lower sites (865 and 1260 m), extensive trail systems already existed, and the forests were partially degraded. The remaining two transect zones, at 1550 and 1950 m, were in undisturbed forest. At each site three transect lines were used to census lemurs. At 865 and 1260 m, we utilized preexisting trails, whereas at 1550 and 1950 m, new trails were cut and laid out. All transects fell within the established project transect zone ±75 m, centered at 865, 1260, 1550, and 1950 m. A minimum of 7 days was spent in all elevational zones.

Census Methods

In each elevational zone three trails of varying lengths (375–1500 m) were used for lemur surveys. Lemurs were censused by walking slowly (approximately 0.6 km/hr) along trails marked every 25 m with flagging tape. Because of the difficult terrain, it was necessary to stop fairly regularly (approximately every 50 m) to watch and listen for lemurs during census walks. When lemurs were detected, we noted the species, number

of individuals, age and sex composition, and general activity of the group, as well as the time of contact, position on the transect, height from the ground, and habitat type. Distance from the observer and perpendicular distance from the trail were estimated for the first individual seen in each group. No more than 10 min were spent for any single sighting. At night, a headlamp, handheld flashlight, and binoculars (7 × 42) were used to detect lemurs (using eye shine) and to view them once detected. Nocturnal censuses began 10–60 min after dusk, whereas diurnal censuses took place at all hours of daylight. Trails were occasionally censused twice during daylight hours, but each walk was always separated by a time interval of at least 6 hr.

Because the number of census walks and the number of sightings were low, no estimates of lemur densities were made (Whitesides et al., 1988). However, mean number of sightings of lemurs per kilometer of transect were calculated. Additionally, the mean of all distances perpendicular to the trail at which lemurs were seen was used to determine the detection distance for each species. For diurnal censuses the mean number of groups and for nocturnal censuses the mean number of individuals observed within the transects were given. Lemur species heard but not seen during census walks or seen outside of census walks by ourselves or other researchers were recorded as being present only. Local people were questioned to collect information about the presence of lemur species.

For all species except the aye-aye *Daubentonia madagascariensis,* direct observation was used. Aye-aye presence was recorded indirectly by finding characteristic feeding signs (gnaw marks from excavation of dead wood or living branches or opened seeds of *Canarium madagascariense*). Furthermore, we paid special attention to vocalizations (songs) of the indris, and when they started to sing we noted the time and the climatic conditions.

Results and Species Account

A list of the lemur species observed within the reserve and their elevational distribution is presented in Table 14-1. A total of 10 lemur species was recorded by direct observation, and evidence of an 11th species, *Daubentonia madagascariensis,* was found at 865 m. None of the four ele-

TABLE 14-1. Primate species of the RS d'Anjanaharibe-Sud listed by elevation (includes species recorded during survey walks, outside survey walks, or in areas not surveyed and species reported to be at a specific altitude by local people).*

Species	865 m	1260 m	1550 m	1950 m
Microcebus rufus	+	+	+	−
Cheirogaleus major	+	+	+	−
Allocebus trichotis	+	−	−	−
Avahi laniger	+	+	−	−
Lepilemur mustelinus	+	+	+	−
Daubentonia madagascariensis	+	−	−	−
Hapalemur griseus	†	+	+	+
Eulemur fulvus	+	+	+	−
Eulemur rubriventer	−	+	+	−
Indri indri	+	−	−	−
Propithecus diadema	†	†	+	−
Total no. of species	8	7	7	1
Total no. of species including local reports	10	8	7	1

* + = species present; − = species absent; and † = species reported by locals.

vational zones contained all species. Rather, at 865, 1260, and 1550 m, the total number of species observed remained relatively constant, but the species composition changed. Eight lemur species were found in the 865 m zone, seven species were found in both the 1260 and 1550 m zones, and *Hapalemur griseus* was the only species found at 1950 m. When the local people's observations were considered, the number of species increased at 865 m from eight to 10 and at 1260 m from seven to eight. The length of transects, altitude, number of census walks, and observed species are listed in Table 14-2 for night censuses and in Table 14-3 for day censuses.

Nocturnal Censuses

Microcebus rufus   Rufous Mouse Lemur

Microcebus rufus was found at 865, 1260, and 1550 m, and the mean number of sightings remained approximately constant across this elevational range (Table 14-2). These lemurs had small ears, the dorsal parts of the body were reddish brown, occasionally with a thin black dorsal stripe, and the ventrum was whitish. They often showed their characteristic bouncy locomotion when moving around in fine branches (approximately 1–3 cm diameter). In general, *Microcebus* were difficult to detect because the vegetation was dense. We often heard them but were unable to see them.

Cheirogaleus major   Greater Dwarf Lemur

Cheirogaleus major was observed from 865 to 1550 m (Table 14-2). Census results showed that at 865 and 1260 m, *C. major* was the most common primate species. One individual of *C. major* was trapped at 865 m with a National trap set for small mammals (for detailed information see Chapter 12). Its dorsal pelage was gray-brown to slightly reddish, and its underparts were paler, almost white. The head was gray-brown, and the eyes were surrounded by marked dark rings. A small patch of white fur was located between the eyes, and the muzzle was dark with reddish nostrils. All but one *Cheirogaleus* observed in the reserve were comparable with the captured animal. The exception was an individual seen at 1260 m; it could have been *C. medius*, but positive identification was not possible. Its upper part was more gray or silver-gray than brown or reddish brown, and the head was also gray. Additionally, this animal was much smaller (about half as large) than any individuals identified as *C. major*.

Cheirogaleus major were generally observed alone on large (approximately 3–10 cm diameter) as well as small (approximately 1–3 cm diameter) branches and rarely descended below 4 m. Some individuals approached us and appeared quite unafraid. Within the 865 m zone, we observed pairs of *C. major* on several night surveys and once observed a group of six individuals (23 October at 19:00 hr). Vocalizing individuals were heard every night at this site and often at 1260 m.

TABLE 14-2. Mean number of sightings of species at nocturnal censuses per kilometer of transect in the RS d'Anjanaharibe-Sud.

Site	Altitude (m)	Length of transects (m)	No. of censuses	Microcebus rufus	Cheirogaleus major	Allocebus trichotis	Avahi laniger	Lepilemur mustelinus	Daubentonia madagascariensis	No. of species
1a	865	1,500	5	0.9	3.7	0.4	0.5	0.8	fd*	6
1b	865	400	5	0	5.5	0.5	0	1	0	3
1c	865	700	5	0.1	3.4	0	0.3	0.3	fd	5
2a	1260	525	5	0.4	0	0	0	1.5	0	2
2b	1260	900	5	1.1	1.8	0	0.2	1.3	0	4
2c	1260	1,000	5	0.2	1.2	0	0	0.4	0	3
3a	1550	650	5	0.6	0	0	0	0.3	0	2
3b	1550	375	5	0	1.1	0	0	0	0	1
3c	1550	500	5	0	0.8	0	0	0.4	0	2
4a	1950	375	5	0	0	0	0	0	0	0
4b	1950	625	5	0	0	0	0	0	0	0
4c	1950	500	5	0	0	0	0	0	0	0
Detection distance, m†				4.2 ± 2.9 N = 17	6.2 ± 4.4 N = 69	4.6 ± 2.3 N = 4	4.8 ± 2.2 N = 6	4.5 ± 3.3 N = 25		

* fd = feeding damage (see text).
† Detection distance indicates the mean distance (±SD) perpendicular to the trail at which lemurs were seen.

Site	Altitude (m)	Length of transect (m)	No. of censuses	Hapalemur griseus	Eulemur fulvus	Eulemur rubriven- ter	Indri indri	Propithecus diadema	No. of species
1a	865	1,500	10	0	*	0	0.06	*	3
1b	865	400	10	0	0.8	0	*	0	2
1c	865	700	10	0	*	0	*	0	2
2a	1260	525	8	0.2	0	*	0	0	2
2b	1260	900	8	0.1	0	0.1	0	0	2
2c	1260	1.000	8	0	0.1	*	0	0	2
3a	1550	650	7	0.2	*	*	0	0.4	4
3b	1550	375	7	0.8	0	0	0	0	1
3c	1550	500	7	*	0	0.3	0	*	3
4a	1950	375	7	*	0	0	0	0	1
4b	1950	625	8	0	0	0	0	0	0
4c	1950	500	8	*	0	0	0	0	1
Detection distance, m†				5.4 ± 2.6 N = 5	11.1 ± 9.9 N = 4	10 N = 2	10 N = 1	4.8 ± 4.6 N = 2	

* Species heard or seen outside the predefined census walks.
† Detection distance indicates the mean distance (±SD) perpendicular to the trail at which lemurs were seen.

Allocebus trichotis Hairy Eared Dwarf Lemur

Four sightings of *Allocebus trichotis* were recorded in the 865 m zone (Table 14-2). A fifth individual was seen on a trail during a noncensus night walk. In general, the dorsal pelage was darkish gray, and the underparts were paler, varying from light gray to almost white, which extended up the sides. A darker but not well defined median dorsal stripe was noticeable in two of the five individuals seen. The head was gray, and the face had a median white stripe running from near the tip of the rostrum to between the eyes. The eyes were surrounded by a narrow dark ring. The small ears were almost not visible, and the ear tufts were generally inconspicuous. However, on one occasion we clearly saw the wavy hair around the ears. The tail was grayish, darkened toward the tip and somewhat bushy. *Allocebus* was smaller than *Cheirogaleus major* but larger than *Microcebus rufus.*

Allocebus trichotis were found at a height of 3–12 m above the ground in lianas and fine branches (approximately 1–3 cm diameter). The means of locomotion was similar to that of *Microcebus.*

Avahi laniger Eastern Woolly Lemur

Avahi laniger was found at 865 and 1260 m (Table 14-2). The dorsal pelage was gray, and the ventral parts were reddish brown. The tail was rusty red and darkened toward the tip. The face was brownish, and a lighter, whitish band above the eyes was visible. At 865 m, one adult pair with a single offspring was observed. The group huddled together in the characteristic resting posture in the fork of a tree, and the infant was carried on the back of one adult.

Lepilemur mustelinus Weasel Sportive Lemur

Lepilemur mustelinus was found within the 865, 1260, and 1550 m zones (Table 14-2). The specific determination was based on its dense, chestnut brown dorsal and ventral pelage and its distally dark tail. Occasionally, a darker median stripe could be distinguished on the back. Considerable variation in body size and body mass was observed. At 1260 m, we found a single *Lepilemur* infant "parked" on a branch. Dorsally its fur was reddish brown, and the ventrum was paler and greyish. The head was also gray and slightly darker on the face. The ears were naked with a dark tip, and the gray tail was unusually short (approximately 10 cm). Three days later and 20 m away from the first sighting, we again observed an infant (likely the same individual) resting in a vertical position. At the same time we detected an adult *Lepilemur,* approximately 4 m away, that

traveled to the infant, groomed it, then carried it away on its back. Apart from this observation, *L. mustelinus* was found alone, generally resting in a vertical position or leaping from one relatively large (10–20 cm dbh) tree trunk to another.

Daubentonia madagascariensis   Aye-aye

Although no *Daubentonia madagascariensis* were observed during the survey, evidence was found that they occur in the RS d'Anjanaharibe-Sud. Two indications were found in the 865 m zone. Three holes (each about 1–1.5 cm diameter) gnawed in a rough-barked tree (18 cm dbh) at 110 cm above the ground were found. The bark around the holes seemed to have been gnawed recently because it was still moist and fresh. Notch marks in the wood around the hole resembled incisor gnaw marks. The marks seemed identical to aye-aye damage found at the RNI de Marojejy in 1988 (Hawkins, pers. comm.). Additionally, numerous seeds of *Canarium madagascariense* (Family Burseraceae) were found at 865 m that had been opened with a technique characteristic of *D. madagascariensis* (Iwano & Iwakawa, 1988; Goodman & Sterling, 1996).

Diurnal Censuses

Hapalemur griseus griseus   Grey Gentle Lemur

Hapalemur griseus was found between 1260 and 1950 m (Table 14-3) and was most abundant at 1550 m. According to the local guides, it also occurs in the 865 m zone. At 1950 m one individual was captured around 15:00 hr in a mist net set for birds (for methodological details see Chapter 8). Its dorsal fur was gray and tipped with brown, the underparts were paler and more brownish, and the crown was brownish red. The ears were totally hidden by surrounding fur. This pelage characteristic generally corresponded with the other gentle lemurs observed during the survey.

Remains of another individual were found on the ground in the 1950 m zone in an area of mossy forest with a high density of bamboo. It is not clear whether the animal died of natural causes or was preyed upon. During census walks in the 1950 m zone, however, *Hapalemur* was nei-

ther seen nor heard. The only two vocalizing individuals of this species at 1950 m were heard outside census walks.

Most sightings of *Hapalemur* were of one or occasionally of two individuals, and none was seen with young. A group of four to six individuals was seen frequently around the 1550 m campsite. They were active in the late afternoon and vocalized a couple of hours before dusk as well as in the predawn hours. One individual was observed feeding on stick bamboo (around 15:00 hr). Branches of bamboo were pulled to the mouth by hand, and the animal chewed off leaf stalks, removing the exterior layers with its teeth before eating.

Eulemur fulvus albifrons   White-fronted Lemur

Eulemur fulvus albifrons were found at 865, 1260, and 1550 m (Table 14-3). Males were darkish brown dorsally, with a black face and white forehead, crown, ears, cheeks, and throat. The fur of the females was gray-brown, and the head was darker gray.

Group size varied from three to five animals (N = 7 groups), and groups moved high in the canopy between 4 and 16 m. Two groups occurred along one trail (1a) in the 865 m zone. The first consisted of two adult males, one adult female, and one subadult, and the second group contained two adult males, two adult females, and a fifth individual of unknown gender and age. Within each elevational zone, adult females were seen carrying single offspring; the single exception was a female at 865 m with twins.

White-fronted lemurs were often heard calling at dusk and occasionally at night. They were seen actively moving in the canopy during all daylight hours and occasionally were observed feeding. Generally, *E. fulvus* fled immediately upon detecting us. However, on a few occasions, adult males in the group displayed aggressively by emitting vocalizations and thrashing the tail rather than fleeing immediately.

Eulemur rubriventer   Red-bellied Lemur

Eulemur rubriventer was found in the 1260 m and 1550 m zones (Table 14-3). The animals were dark brown dorsally, with reddish brown underparts. The face was dark, and males had a char-

acteristic white patch below each eye. Females had white markings under the neck and chin.

At 1260 m three groups were found. The first group consisted of three males, two females, and one young carried on the mother's belly; the second, three females; and the third, one female, one male, and a juvenile. Once, two males were seen chasing each other up and down trees and biting each other, coming to within 1 m of the ground at one point. The relationship between these two individuals was unknown. One group was found in the 1550 m zone and consisted of two adult pairs, one with an infant (carried ventrally by an adult male), and two juvenile/subadult animals.

Indri indri **Indri**

Indri was found only in the 865 m zone (Table 14-3). One group consisting of two individuals was seen on 10 census walks. On the basis of all individuals we observed, including animals seen outside predefined census walks, the predominate fur color was black with white or whitish patches on the crown, flanks, and forelimbs.

A total of at least five groups of *Indri* could be heard from the 865 m zone (some of these were calling from well outside the zone, given that their calls travel long distances). *Indri* songs were generally heard in the morning between 5:30 and 11:50 hr and on a few occasions in the afternoon. Between 18 and 30 October a total of 97 *Indri* calling bouts were registered. The songs were recorded mostly when it was sunny (52.6%) but also when it was cloudy (37.0%) or rainy (10.4%).

Propithecus diadema candidus **Silky Sifaka**

Propithecus diadema was seen in the 1550 m zone on two occasions. The skin of the hairless face was black, and the dense body pelage was completely white. Also at 1550 m, one adult-sized individual with a single infant carried ventrally was seen outside a census walk. Another individual could be heard nearby producing the "sifaka" vocalization but was not seen. A single *P. diadema* was observed in a tree about 1.5 km from the campsite in the 865 m zone. We were told by the local inhabitants that it also occurs in the 1260 m elevation area. Whenever *Propithecus* were

seen (N = 4), they fled immediately, calling continuously.

Species Accumulation Curves

No additional species were seen during nocturnal censuses in the 865 and 1550 m zones after the first 3–4 hr of observation (Fig. 14-1a, 14-1c), whereas in the 1260 m zone 11 hr were needed to reach a plateau (Fig. 14-1b). This could have been due to the fact that rain and fog interfered with sampling on the first 8 hr of the census nights in the 1260 m elevation. For diurnal censuses, no new species were accrued in the 865 and 1260 m zones after 15–20 hr of observation (Fig. 14-1a, 14-1b). The species accumulation curve for lemurs recorded during diurnal censuses in the 1550 m elevation zone, however, reached its plateau after 32 hr of observation (Fig. 14-1c). We did not see all lemur species present at any site, during either diurnal or nocturnal censuses.

Discussion

Nicoll and Langrand (1989) listed seven lemur species for the RS d'Anjanaharibe-Sud. On the basis of our survey results, an additional four species, *Allocebus trichotis, Lepilemur mustelinus, Daubentonia madagascariensis,* and *Eulemur rubriventer,* also occur in the reserve. This species diversity is average for lemurs in eastern humid forest reserves for which reliable data are available. Nine species are known in RNI de Marojejy, and 10 species are known on the Masoala Peninsula (Table 14-4). *Microcebus rufus, Cheirogaleus major, L. mustelinus,* and *E. fulvus* are present in all of the protected areas listed in Table 14-4.

The sighting at 1260 m of the *Cheirogaleus,* which could have been *C. medius,* is difficult to assess. According to Tattersall (1982), both *Cheirogaleus* species are found in eastern humid forest, but so far there have been no reports of sympatry. Thus, if *C. medius* does occur in the RS d'Anjanaharibe-Sud, it is doubtless very rare compared with *C. major,* which is common in this forest.

After the rediscovery of *Allocebus trichotis* in 1989 around Mananara (Meier & Albignac, 1991), only a few records of it were reported. Until recently, knowledge of this species was based
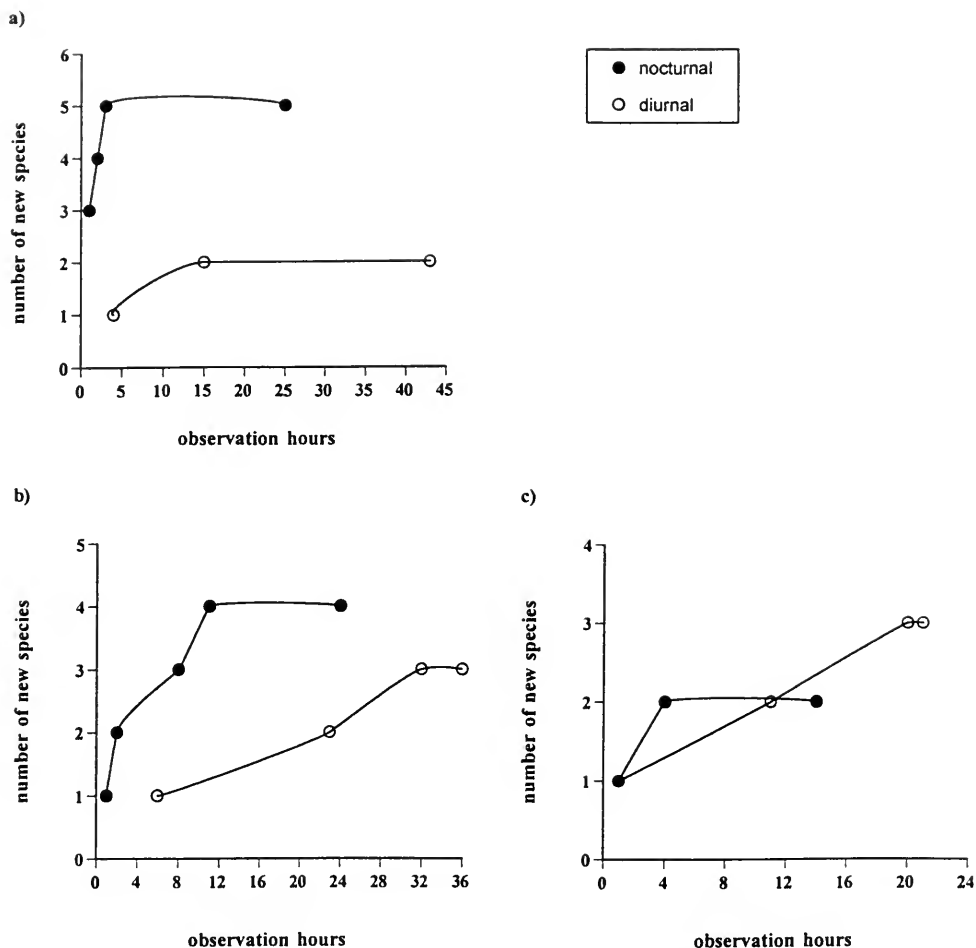
FIG. 14-1. Species accumulation curves in the 865 m (**a**), 1260 m (**b**), and 1550 m (**c**) elevation zone of lemur species seen during nocturnal and diurnal census walks. The last value of each curve represents the total number of observation hours.

on five existing museum specimens housed in three collections (see Meier & Albignac, 1991). One of the rediscovered animals was found in degraded primary lowland rain forest close to the village of Ambavala, 16 km from Mananara on a bearing of 250°, and another three animals were found 10 m from a 2-year-old clearing in primary lowland rain forest, located 37 km from Mananara on a bearing of 204°. In the RS d'Anjanaharibe-Sud, *A. trichotis* was recorded only within the 865 m zone. The area around the 865 m camp was also partly disturbed by selective logging and an extensive trail system. Thus, it appears that *A. trichotis* is at least partially tolerant of forest disturbance. Furthermore, its distributional range is more widespread than presented in the current literature. It has recently been recorded in Masoala

Peninsula (Sterling & Rakotoarison, in press), and it has been seen and captured in the lowland forest of the RNI de Zahamena (Rakotoarison, unpubl. data). Moreover, this species was discovered in a highland rain forest in the central/eastern area of Madagascar in the Forêt de Vohidrazana, an unprotected area near Andasibe-Périnet (Rakotoarison et al., 1996). Sightings in those areas contradict the idea of Meier and Albignac (1991) that *Allocebus* is probably limited to lowland rain forest. In any case, *A. trichotis* in the RS d'Anjanaharibe-Sud warrants further study. If more is known about its ecology and distribution, chances of this species' survival will be increased.

Avahi laniger has been reported in numerous protected reserves (Mittermeier et al., 1994), providing a good picture of its latitudinal range.

TABLE 14-4. List of lemurs that are present in different protected areas along the eastern humid forests.*

	RNI de Marojejy[1]	RS d'Anjanaharibe-Sud	Masoala Peninsula[2]	RB de Mananara[4]	RNI de Betampona[2]	RNI de Zahamena[2]	RS d'Analamazaotra[2]	PN de Ranomafana[2]	RNI d'Andringitra[6]
Microcebus rufus	+	+	+	+	+	+	+	+	+
Allocebus trichotis		+	+[3]	+		+[5]			
Cheirogaleus major	+	+	+	+	+	+	+	+	+
Phaner furcifer			+		+	+			
Lepilemur sp.									
Lepilemur microdon								+	+
Lepilemur mustelinus	+	+		+	+	+	+		
Avahi laniger	+	+	+		+	+	+	+	+
Daubentonia madagascariensis	+	+	+	+	+	+	+	+	+
Hapalemur simus								+	+
Hapalemur griseus griseus	+	+	+	+	+	+	+	+	+
Hapalemur aureus								+	+
Eulemur fulvus subsp.									
Eulemur fulvus fulvus				+			+		
Eulemur fulvus albifrons	+	+	+		+	+			+
Eulemur fulvus albocollaris									
Eulemur fulvus rufus								+	+
Eulemur rubriventer	+	+				+	+	+	+[7]
Lemur catta									
Varecia variegata subsp.				+					
Varecia variegata rubra			+						
Varecia variegata variegata					+	+	+	+	+
Propithecus diadema diadema				+	+	+			
Propithecus diadema candidus		+							
Propithecus diadema edwardsi								+	+
Indri indri	+	+	+	+	+	+	+		
Total no. of species	9	11	10	10	11	13	10	12	13

* PN = Parc National; RB = Réserve de la Biosphère; RNI = Réserve Naturelle Intégrale; RS = Réserve Spéciale; and + = species present.
[1] Duckworth et al. (1995).
[2] Mittermeier et al. (1992).
[3] Sterling & Rakotoarison (in press).
[4] Nicoll and Langrand (1989).
[5] Rakotoarison et al. (1996).
[6] Sterling and Ramarason (1996).
[7] Goodman and Langrand (1996).

However, little is known about its elevational distribution. Our sighting of one individual at 1260 m in the RS d'Anjanaharibe-Sud is the first record of *A. laniger* at this altitude, indicating that the species occupies a greater elevational range than previously reported.

Hapalemur griseus is found throughout all remaining eastern rain forests wherever bamboo is present (Tattersall, 1982). Thus, it is not suprising that we found *H. griseus* at 1950 m in the RS d'Anjanaharibe-Sud since the main vegetation type at this altitude was bamboo. In the RNI de Tsaratanana, *H. griseus* was also recorded at 2050 m (Albignac, 1970). *Hapalemur griseus* usually lives in groups of two to five individuals, but occasionally single animals and much larger aggregations occur (Petter et al., 1977; Pollock, 1986a; Tattersall, 1982). In the RS d'Anjanaharibe-Sud, however, we saw single individuals most of the time. Furthermore, during the survey, no *Hapalemur* were seen with young. In the RS d'Analamazaotra, *Hapalemur* were observed with small but independently moving young in November and January (Petter & Peyrieras, 1970). These authors reported the start of the birth season as in late October and continuing to January.

Eulemur rubriventer is found throughout the eastern rain forest from the RNI de Tsaratanana to the RNI d'Andringitra Massif, and it is reported to prefer higher altitudes (Petter et al., 1977; Tattersall, 1982; Overdorff, 1992). Albignac (1970) found them at 2400 m elevation in the forest of the RNI de Tsaratanana. In the RS d'Anjanaharibe-Sud, however, *E. rubriventer* occurred only between the 1260 and 1550 m zones. In the 1260 m zone we observed an aggressive behavior (chasing and biting) between two males. Dague and Petter (1988) found little evidence of territoriality in *E. rubriventer,* and no aggressive or avoidance behavior between groups was noticed. According to Overdorff (1992, 1993), however, Red-bellied lemurs are territorial. The author showed that Red-bellied lemurs maintain exclusive use of their home range and that they defend the boundaries actively against intrusion by neighboring groups.

Eulemur fulvus albifrons have been seen in groups of between three and six animals in the RNI de Zahamena (Raxworthy, 1986). In the RNI de Marojejy most groups consisted of 10–12 individuals, and both number of groups and group size of *E. f. albifrons* were lower in disturbed areas with high hunting pressure compared with areas with less hunting (Duckworth et al., 1995). The absence of groups larger than five individuals

in the RS d'Anjanaharibe-Sud could reflect hunting pressures in this area. According to local people, *E. f. albifrons* is hunted, and in the 865 and 1260 m zones, lemur traps were found in clearings along hill crests.

The RS d'Anjanaharibe-Sud appears to be the near northern modern limit of *Indri* on Madagascar. *Indri* have not been found in the RNI de Marojejy, which is only about 100 km further northeast (Duckworth et al., 1995). According to Thalmann et al. (1993), indris in the north are black with a light face ring, and the outer sides of the lower arm and the leg are black. However, our description was based mainly on two individuals we observed for less than 1 min. Thus, we could not make any obvious and clear statement about the fur pattern of the indris in this region. Researchers have suggested that *Indri* sing more frequently just before rain (Pollock, 1986b; Thalmann et al., 1993). In the RS d'Anjanaharibe-Sud, however, we did not find any evidence of this pattern.

The low encounter rate for *Propithecus* during the survey was striking, and our local guides mentioned that this species is rare in the whole RS d'Anjanaharibe-Sud. It is possible that hunting and fear of humans are responsible for their low numbers. *Propithecus diadema candidus* occurs throughout the humid belt north of Maroantsetra to the Andapa Basin (Tattersall, 1982). It was common in the RNI de Marojejy, where nine different groups were seen at the 800 m zone and three were seen at higher altitudes (up to 1400 m) (Duckworth et al., 1995). At 300 m, however, no groups of *Propithecus* were recorded, and the authors mentioned that this could have been due to the degraded state of the forest, hunting pressure, or an altitudinal preference.

There was elevational variation in species richness on the slopes of the RS d'Anjanaharibe-Sud (Table 14-1). At the 865 m site a total of eight species were recorded; seven were recorded at the 1260 and 1550 m sites. The most dramatic change was found toward the summit of the mountain, where species richness dropped from seven species at 1550 m to one species at 1950 m. The vegetation of the latter zone was characterized by a high density of bamboo and bamboo vines, a principal food of *Hapalemur. Hapalemur* are known to range in all habitats that contain bamboo, including stream edges and ridges (Wright, 1986). There was no evidence of *Microcebus* at 1950 m although it has previously been observed from lowland forests to montane forests at high altitudes (Petter & Petter-Rousseaux, 1964; Tattersall, 1982).

Considerable differences in the mean number of sightings of lemur species were found in the four elevational zones. Although a species may have been present in more than one elevational zone, frequency of detection often differed greatly. For example, *Cheirogaleus major* was seen often at 865 m, whereas at 1260 and 1565 m the number of sightings was much lower (Table 14-2). The number of sightings of *Microcebus* and *Lepilemur* remained almost constant in the two lowest elevational zones but decreased at 1550 m. However, according to the species accumulation curves, the hours of observation needed for detection of the majority of lemur species at each site in the RS d'Anjanaharibe-Sud varied between 15 and 32 hr for diurnal censuses and between 3 and 11 hr for nocturnal censuses (Fig. 14-1a–c). These variations may have been due to differences in the climatic conditions, therefore, it is difficult to compare absolute numbers of sightings of lemur species between sites.

The major problem of the species accumulation curves, however, is that the number of species observed at each site did not represent complete primate communities. Observed differences in species composition between elevational zones, especially for diurnal censuses, are more likely artifacts of sampling error than the results of altitudinal distribution. It seems unlikely that *Propithecus diadema* were not found at 1260 m altitude, even after 36 diurnal census hours, and that *Hapalemur* did not show up at 865 m. Furthermore, during the diurnal censuses at 1260 and 1550 m, new species were added only a few hours before observations were finished, and it therefore also seems unlikely that the accumulation curves actually "leveled out" (Fig. 14-1). Thus, the species accumulation curves, which imply that asymptotes were reached, are misleading. If the observations of local people are considered, the survey did not include all species that might occur at any one site. The survey was too short, its purpose being a rapid assessment of the primate community of the RS d'Anjanaharibe-Sud rather than a complete inventory of lemurs.

At 865 and 1260 m numerous trails existed before our survey. From our camps, we could sometimes smell smoke from nearby fires associated with slash and burn agricultural practices. Areas of forest at 1260 m had been degraded by mining for semiprecious stones, leaving many small and some large clearings. People working on mines and living within and around the reserve hunt lemurs for food. Most of the clearings we found along existing trails, particularly on hill crests, contained lemur traps. Traps were composed of a horizontal branch (about 3 cm in diameter) fixed at a height of about 2–3 m. None of the traps we found was in functional condition, but when working, a noose of rope, placed the middle of the branch, catches and strangles lemurs as they walk along the branch. These traps are specialized for catching quadrupedally moving lemurs, such as *Eulemur fulvus*. According to local people, *E. fulvus*, as well as *Propithecus diadema*, are not protected by "fady" (taboo) and are hunted. *Indri indri*, on the other hand, have some protection based on local taboo (Thalmann et al., 1993), at least as long as hunters are members of the local cultural group. Human pressures within the RS d'Anjanaharibe-Sud have increased recently with the construction of a road through the reserve. Penetration into the reserve is now much easier, and lemurs are likely to come under increasing pressure.

The high diversity of lemurs found in the forests of the RS d'Anjanaharibe-Sud clearly demonstrates the importance of this area within the network of protected areas of Madagascar. Some of the rarer lemur species, especially *Allocebus trichotis, Propithecus diadema candidus,* and *Daubentonia madagascariensis,* occur in the reserve. Protection of RS d'Anjanaharibe-Sud would require more effective guarding with sufficient equipment, development of alternatives to current agricultural practices, and programs designed to enable local human populations to maintain a decent standard of living without degrading the forest.

Acknowledgments

Literature Cited

ALBIGNAC, R. 1970. Mammifères et oiseaux du massif du Tsaratanana. Mémoires ORSTOM, **37:** 223–229.

BOURLIERE, F. 1985. Primate communities: Their structure and role in tropical ecosystems. International Journal of Primatology, **6:** 1–26.

DAGUE, C., AND J. J. PETTER. 1988. Observations sur le *Lemur rubriventer* dans son milieu naturel, pp. 78–89. *In* Rakotovao, L., V. Barre, and J. Sayer, eds., L'équilibre des Ecosystèmes Forestiers de Madagascar: Actes d'un séminaire international. International Union for the Conservation of Nature and Natural Resources, Gland and Cambridge. 338 pp.

DUCKWORTH, J. W., M. I. EVANS, A. F. A. HAWKINS, R. J. SAFFORD, AND R. J. WILKINSON. 1995. The lemurs of Marojejy Strict Nature Reserve, Madagascar: A status overview with notes on ecology and threats. International Journal of Primatology, **16:** 545–559.

GOODMAN, S. M, AND O. LANGRAND. 1996. A high mountain population of the ring-tailed lemur *Lemur catta* on the Andringitra Massif, Madagascar. Oryx, **30:** 259–268.

GOODMAN, S. M., AND E. J. STERLING. 1996. The utilization of *Canarium* (Burseraceae) seeds by vertebrates in the Réserve Naturelle Intégrale d'Andringitra, Madagascar, pp. 83–89. *In* Goodman, S. M., ed., A floral and faunal inventory of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: With reference to elevational variation. Fieldiana: Zoology, n.s., **85:** 1–319.

HARCOURT, C., AND J. THORNBACK. 1990. Lemurs of Madagascar and the Comores. The IUCN Red Data Book. International Union for the Conservation of Nature and Natural Resources, Gland and Cambridge.

IWANO, T., AND C. IWAKAWA. 1988. Feeding behavior of the aye-aye (*Daubentonia madagascariensis*) on nuts of Ramy (*Canarium madagascariensis*). Folia Primatologica, **50:** 136–142.

MEIER, B., AND R. ALBIGNAC. 1991. Rediscovery of *Allocebus trichotis* Günther 1875 (Primates) in northeast Madagascar. Folia Primatologica, **56:** 57–63.

MITTERMEIER, R. A., I. TATTERSALL, W. R. KONSTANT, D. M. MEYERS, AND R. B. MAST. 1994. Lemurs of Madagascar. Conservation International, Washington, D.C.

NICOLL, M. E., AND O. LANGRAND. 1989. Madagascar: Revue de la Conservation et des Aires Protégées. World Wide Fund for Nature, Gland.

OVERDORFF, D. J. 1992. Territoriality and home range use by red-bellied lemurs (*Eulemur rubriventer*) in Madagascar. American Journal of Primatology, **16:** 143–153.

OVERDORFF, D. J. 1993. Ecological and reproductive correlates to range use in red-bellied lemurs (*Eulemur rubriventer*) and rufous lemurs (*Eulemur fulvus rufus*): pp. 167–178. *In* Kappeler, P. M., and J. U. Ganzhorn, eds., Lemur Social Systems and Their Ecological Basis. Plenum Press, New York, 274 pp.

PETTER, J.-J., R. ALBIGNAC, AND Y. RUMPLER. 1977. Mammifères lémuriens (Primates prosimiens). Faune de Madagascar, vol. 44. ORSTOM-CNRS, Paris.

PETTER, J.-J., AND A. PETTER-ROUSSEAUX. 1964. Première tentative d'estimation des densités de peuplement des lémuriens malgaches. La Terre et al Vie, **18:** 427–435.

PETTER, J.-J., AND A. PEYRIERAS. 1970. Observations Eco-Ethologiques sur les lémuriens malgache du genre *Hapalemur*. La Terre et la Vie, **24:** 356–382.

POLLOCK, J. I. 1986a. A note on the ecology and behavior of *Hapalemur griseus*. Primate Conservation, **7:** 97–100.

———. 1986b. The song of the indris (*Indri indri*; Primates: Lemuroidea): Natural history, form, and function. International Journal of Primatology, **7:** 225–267.

RAKOTOARISON, N., H. ZIMMERMANN, AND E. ZIMMERMANN. 1996. Hairy-eared dwarf lemur (*Allocebus trichotis*) discovered in a highland rain forest of eastern Madagascar, pp. 275–282. *In* Lourenço, W. R., ed. Biogéographie de Madagascar. ORSTOM Editions, Paris.

RAXWORTHY, C. 1986. The lemurs of Zahamena Réserve. Primate Conservation, **7:** 46–48.

STERLING, E. J., AND N. RAKOTOARISON. In press. Rapid assessment of primate species richness and density on the Masoala Pensinsula, eastern Madagascar. Folia Primatologica.

STERLING, E. J., AND M. G. RAMAROSON. 1996. Rapid assessment of the primate fauna of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar, pp. 293–305. *In* Goodman, S. M., ed., A floral and faunal inventory of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: With reference to elevational variation. Fieldiana: Zoology, n.s., **85:** 1–319.

TATTERSALL, I. 1982. The Primates of Madagascar. Columbia University Press, New York.

THALMANN, U., T. GEISSMANN, A. SIMONA, AND T. MUTSCHLER. 1993. The indris of Anjanaharibe-Sud (NE-Madagascar). International Journal of Primatology, **14:** 357–381.

WRIGHT, P. 1986. Diet, ranging behavior and activity pattern of the gentle lemur (*Hapalemur griseus*) in Madagascar. American Journal of Physical Anthropology, **69:** 283.

WHITESIDES, G. H., J. F. OATES, S. M. GREEN, AND R. P. KLUBERDANZ. 1988. Estimating primate densities from transects in a West African rain forest: A comparison of techniques. Journal of Animal Ecology, **57:** 345–367.

Gazetteer of Localities Mentioned in the Text*

Locality	Elevation (m)	Latitude S °	Latitude S ′	Longitude E °	Longitude E ′
Ambanizana		15	37	49	58
Ambatomainty	1400	14	45	49	28
Ambatomainty River	1250	14	45	49	28
Ambatovaky, RS		~16	51	~49	08
Ambavala		16	12	49	37
Amboanara		not located			
Ambohimitombo	1200–1500	20	43	47	26
Ambohitantely, RS	1448–1662	18	09	47	16
Ampitambe	900–1300	~20	22	~47	46
Analamazaotra, RS	930–1040	18	56	48	25
Andapa	550	14	40	49	39
Andasy Voalahany	1200	14	44.8	49	28.4
Andohahela, RNI					
Parcel 1		~24	40	~46	40
Parcel 2		~24	53	~46	33
Andramanalana	2260	14	24	49	20
Andramonta River		14	37	49	30
Andranotsarabe	980	14	45	49	29
Andringitra, RNI		~22	14	~46	54
Andromena River		14	44	49	30
Andronobe Field Station		15	41	49	57
Androranga River		14	11	49	44
Anjanaharibe Anivo	2064	14	44	49	27
Anjanaharibe-Nord	1899	14	37	49	24
Anjanaharibe-Sud, RS	500–2064	~49	26	~14	42
Anjavadilava	1800–2100	22	09	46	57
Anjavidy Be	1540	14	44.4	49	27.6
Ankafana Forest	1600	21	12	47	12
Ankafina Forest		see Ankafana Forest			
Ankaibe River		14	40	49	37
Ankaratra Massif	2642	19	25	47	12
Anosy Mountains		see Anosyenne Mountains			
Anosyenne Mountains		~24	35	46	45
Antainambalana River		14	46	49	26
Antanamangotraka	800	14	43	49	40
Antongil, Baie		15	45	49	50
Antsahamifelana		14	46	49	28
Antsiranana		12	16	49	17
Bealanana		14	33	48	44
Befingitra		see Befingotra			
Befingotra	680	14	43	49	32
Behondroko, Mt.		see Beondroka			
Beondroka, Mt.		14	24	49	47
Betaolana	700–1051	14	31	49	29
Camp 1	875	14	45.3	49	30.3
Camp 2	1260	14	44.7	49	27.7
Camp 3	1550	14	44.5	49	26.5
Camp 4	1950	14	44.8	49	26.0
Fanovana	600–800	18	55	48	34
Farafangana	0–40	22	49	47	50
Grotte d'Andrahomana	50	25	50	46	40
Hiaraka		15	30	49	56
Ikongo		21	44	47	16
Ivohibe, RS		~22	31	46	59
Lac Alaotra		17	30	48	30
Lohariandava		18	48	48	41
Lokoho River		14	37	49	44

Gazetteer (Continued)

Locality	Elevation (m)	Latitude S °	Latitude S ′	Longitude E °	Longitude E ′
Mahilaka		13	48	48	19
Mananara		16	10	49	46
Mandritsarakely		14	44	49	30
Manjakatompo	1550–1980	19	22	47	26
Manohilahy		17	16	48	01
Manongarivo, RS	155–1876	~13	59	~48	23
Mantady, PN		~18	51	~49	27
Maroantsetra		15	26	49	44
Marojejy, RNI	75–2133	~14	11	~48	57
Marolakana River		14	46	49	29
Marolakana (village)	910	14	46	49	29
Maromiza	1100	18	58	48	27
Midongy du Sud		23	35	47	01
Montagne d'Ambre, PN	850–1475	~12	32	~49	10
Nandihizana	1340	~20	50	~47	10
Nosy Be		13	20	48	15
Périnet		see RS d'Analamazaotra			
Ranomafana (Marolakana)		14	45	49	32
Ranomafana, PN	800–1200	~21	16	~47	28
Sihanaka Forest		~18	07	~48	32
Tsaratanana, RNI	227–2876	~14	26	~49	46
Vinanitelo	1300	21	43	47	16
Vohémar		13	21	50	01
Vohidrazana, Forêt de		18	59	48	32
Vohimena Mountains		~24	35	47	00
Volotsangana River		22	12	46	58
Vondrozo		22	49	47	20
Zahamena, RNI	750–1512	~17	40	~48	50

* For geographical localities such as rivers, large reserves, and mountain ranges, we give an intersection of coordinates that allows for easy location on maps. Information presented in the Gazetteer is based partially on coordinates given by the U.S. Board on Geographic Names (1955) and Viette (1991). PN = Parc National; RNI = Réserve Naturelle Intégrale; and RS = Réserve Spéciale.

Literature Cited

U.S. BOARD ON GEOGRAPHIC NAMES. 1955. Madagascar, Réunion and the Comoro Islands. Gazetteer 2. U.S. Government Printing Office, Washington, D.C.

VIETTE, P. 1991. Principales localités où des Insectes ont été recueillis à Madagascar. Faune de Madagascar, supplément 2. Private printing.

Index to Scientific Names